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BY  
A. G. TANSLEY

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WITH FOURTEEN PLATES, AND NUMEROUS FIGURES  
IN THE TEXT



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LIST OF ERRATA in VOLUME XIII, No. 1, January 1925  
of *Journal of Ecology*

- Page 10, line 7. For "puchella" read "pulchella."  
,, 11, lines 3 and 4. Form subnigrescens and var. alpina should go under *Cetraria*  
    *aculeata*.  
,, 12, line 10 from bottom. For "blytii" read "blyttii."  
,, 13, line 6 from bottom. For "caespititia" read "caespiticia."  
,, 17, line 1. For "Sedges" read "Ledges."  
,, 17, line 24. For "ithyphalla" read "ithyphylla."  
,, 18, line 23. For "orthorrhyncum" read "orthorrhynchum."  
,, 18, line 33. For "ithyphalla" read "ithyphylla."  
,, 19, line 14. For "Topfieldia" read "Tofieldia."  
,, 23, line 28. For "blytii" read blyttii."

THE BRYOPHYTES AND LICHENS OF  
ARCTIC-ALPINE VEGETATION

BY W. WATSON.

## INTRODUCTION.

The account of arctic-alpine vegetation given in *Types of British Vegetation* (18) deals chiefly with the phanerogamic constituents, though the importance of the part played by mosses and lichens is often alluded to. Many of the arctic alpine communities are known to have an abundant and diverse cryptogamic flora, and bryophytes often form the chief constituents. In this paper the bryophytes and lichens are chiefly dealt with; the higher plants are only mentioned where they are necessary to a proper correlation with the results of phanerogamic workers. The classification adopted in *Types* is generally followed. W. G. Smith (18, pp. 288-91) gives sound reasons for naming the vegetation of the higher mountains of Scotland arctic-alpine rather than alpine, and these are borne out by an examination of the cryptogamic species found on the Breadalbane and Cairngorm mountains. The climate and the consequent vegetation are neither alpine nor arctic but show characters belonging to both zones. In a general way the lichens and bryophytes are similar to those found on the Alps at corresponding altitudes corrected for latitude. For example, the species found at an altitude of 7000-8000 feet on the rocks and rock-débris of the Grimsel Pass are largely the same as those found on the higher parts of Ben Lawers (3000-4000 feet), but as in the case of flowering-plants some of the "Highland" species of the Scotch mountains descend almost to sea-level and some must be considered arctic rather than alpine plants. As examples of such arctic species may be mentioned *Bryum arcticum*, *Conostomum boreale*, *Timmia norvegica*, *Anthelia juratzkana*, *Chandonanthus setiformis*, *Gymnomitrium alpinum*, *Lophozia kunzeana*, *L. obtusa*, *Moerckia blytii*, *Sphenolobus saxicolus*, *Lecidea alpestris*, *L. arctica*, *Lecanora epibryon*, *L. tartarea* var. *frigida* and *Lopadium* (*Sporopodium*) *fecundum*. On the other hand, the relative distribution and variability of the species correspond more to an alpine district than to an arctic one and this correspondence to alpine vegetation is more pronounced in the cryptogamic vegetation of the higher mountains of England and Wales.

The arctic-alpine vegetation of the British Isles is best shown in the Highlands of Scotland but it is also displayed in the high mountainous ranges of N. Wales and of the Lake District. The Scotch mountains personally explored in detail were Ben Lui (Laoigh), Ben Doran, Ben Chuirn, Meall

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Odhar in the neighbourhood of Tyndrum, and Ben Lawers, Ben Eachan, and Meall nan Tarmachan in the Killin district. During my Scottish investigations the weather conditions were very favourable, but the same cannot be said of the conditions prevailing during my work on the Welsh mountains. On the Glyders the weather was sometimes kind but only on one or two occasions has my work on the summit of Snowdon been carried on whilst the sun was smiling. Wind, rain, or mist rendered the conditions unhappy ones to work in, and these are the normal conditions in which the plants live. Cader Idris and the mountains near Dolgelly also yielded some interesting results, though their vegetation, except for the plateaus, corresponds more to that of the lower alpine and subalpine zones. The mountains of the Lake District have also been visited by me but only a preliminary survey was made. A more detailed examination of the Old Man of Conistone was carried out, but as this is only 2500 feet high (latitude  $53^{\circ}$ ) the vegetation is chiefly of a subalpine character. Dartmoor, although its highest mountain is little more than 2000 feet and its latitude under  $51^{\circ}$ , shows more alpine characters in its vegetation than some equally high mountains further north. This is owing to its peculiar climate, cold rains and mist being frequent. Still it cannot be considered as having an alpine vegetation.

In regard to the distribution of the hepatics in Scotland, Macvicar considers that "the lower limit of altitude does not appear to be appreciably affected by latitude on the mainland except to a very limited extent" (11), and attaches more importance to the more or less vertical distribution of the January isotherms. This is no doubt generally true for hepatics, since humidity is usually a more important factor than summer temperature for them, but the statement cannot be applied to most of the mosses and lichens and I am inclined to think that he minimises the influence of latitude even in regard to hepatics. At any rate, in a consideration of the altitudinal limits of the cryptogamic vegetation of our islands, due regard must be paid to latitude though other factors modify its influence. In the table (p. 22) showing the altitudinal distribution of bryophytes and lichens the latitude is taken as that of Perthshire, and approximate corrections have been made where necessary. Many of the plants are so minute that they are liable to be overlooked and their distribution in our islands is probably very incompletely known. For some of these, data have been obtained from their occurrence on the Swiss Alps, and their probable altitudinal distribution indicated by commas or interrupted lines. In such cases corrections for latitude have been necessary, and of course, can be approximate only, since latitude is not the only character to be taken into account and correlations are always difficult, especially when one of the regions is insular and the other continental. The continual presence of snow on the Swiss Alps tends to lower the heights corresponding to those of our greater latitudes but this tendency is often more than counterbalanced by the more intense sunlight and its longer duration. The corresponding heights will

also vary according to the localities compared. The latitudes of Pontresina and Gletsch are not very different but the vegetation at 7000 feet is more alpine at the latter place than at the former, largely because of the proximity of the Rhone Glacier.

In comparing the cryptogams of the Swiss Alps with those of our high mountains, the absence or rarity of calcicolous plants on the British mountains is especially noticeable. There is very little limestone in our alpine regions and, though a few calcicolous species occur on the schists, they are never so abundant as in some of the calcareous tracts of the Swiss Alps. Most of our alpine soils will have a low pH value<sup>1</sup> though I am not aware of any definite estimations. Sager (14a) has recently obtained the pH values of a number of soils in the Alps. The soil of a heath similar to a *Racomitrium* heath had a pH value of 4.9; another habitat comparable to that of our rock-ledges had a pH of 5.3, whilst the soil with *Polytrichum sexangulare* (snow-patch vegetation) had a pH of 5.2. An estimation of the acidity of the soil on which *Salix herbacea* grew gave a value of 6.3, which is higher than that from the Polytrichetum. In snow-patch vegetation *Salix herbacea* and *Polytrichum sexangulare* may occur together and in the following account are placed in the same community. There are however some reasons for differentiating between these two facies (14) though one must not conclude that a higher pH value is a character constantly separating *Salicetum herbaceae* from Polytrichetum.

The lists of plants characteristic of different associations chiefly consist of bryophytes and lichens, the algae and fungi not having been sufficiently investigated. Some of the algae collected on the Scotch mountains in 1913 were determined by the late W. West but all of them were species which are found at lower altitudes, and the collections were insufficient to afford detailed information as to the algal constituents of the various associations. G. S. West (25) has a few notes of interest: "*Zygnema ericetorum* occurs at all altitudes but is seen in greatest abundance on peat-moors" where it forms "extensive felt-like masses": "altitude has a decided effect upon the algae of a Sphagnum-bog," particularly in regard to the desmids. The diatom *Navicula borealis* is stated to be a conspicuous feature of the algal associations which occur among the mosses of wet rocks at an altitude above 1000 feet. His account of the algae of cryoplankton is chiefly concerned with the polar regions and the continental ice-fields. *Botryococcus braunii* (*Ineffigiata neglecta*) and a number of other algae are given by Crampton and Macgregor (5) as occurring in the dubh-lochans or peat-holes of Ben Armine, but none of the species listed are limited to, or characteristic of, alpine regions. In a recent article (1) on the algae of part of the French Alps, Allorge and Denis state: "On peut donc parler, pour les Algues comme pour les Plantes vasculaires, d'un 'element' arctico-alpin bien différencié," and a list is given. Out of the 17 species

<sup>1</sup> Low and high refer to the negative indices of acidity. The actual acidities are in the reverse order.



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given, 12 occur in Yorkshire (24) and some of them at fairly low levels. Apart from the actual snow-flora (8a) very little definite information as to algae which are confined to the arctic-alpine zone, or rare elsewhere, is available.

The lower arctic-alpine formation and many of the smaller associations or consociations (19) are not dealt with here as their bryophytes and lichens have not been investigated in detail. Some information as to the cryptogamic constituents of a few of the different associations is given by Crampton and Macgregor (5).

##### CONDITIONS OF GROWTH.

The conditions under which plants grow in arctic-alpine districts are dealt with in various works (2, 15, 18, 20, etc.) but they have been considered in regard to phanerogamic plants with root and shoot systems which render the problem of existence in arctic-alpine habitats much more difficult for them than it is for most cryptogams. The terms xerophyte, mesophyte and hydrophyte are not exactly equivalent in meaning in the two groups. The resistance to fatal injury is greater in lower organisms than in more highly specialised ones. This is well known in the animal world and Irmischer (9) has given some details of the greater endurance of drought and cold by the lower plants. The cell is the unit of life and with greater specialisation there is a greater possibility of cells vital to the organism being killed; this involves the death of the individual though some of its cells may still be alive. The chief specialisation in the lower plants is in regard to reproductive bodies, and if sexual cells are necessary the endurance of the plant may be determined by the endurance of these cells. The conditions may not prevent the ordinary vegetative processes occurring but may inhibit the reproductive. Water is essential for sexual reproduction in mosses and liverworts and a plant may have xerophytic vegetative characters though unable to withstand prolonged drought during its reproductive phase. So many of the lower plants appear to be so little dependent on sexual reproduction that this consideration has been treated with less respect than it deserves. The rarity or absence of some apparently xerophytic plants in some districts may perhaps be explained in this way. *Racomitrium lanuginosum* seems admirably fitted (21) to occur in dry places, and certainly it can withstand prolonged drought in certain situations, but in some dry alpine districts it appears to be uncommon (23). It is a plant which does not often produce capsules, though when it does so they are abundant, and the occasional production of capsules may be a necessary factor for the continuance of the plant.

It is then desirable to know how the conditions under which the plants live are produced, to consider the relations between these conditions and the vegetation, and to study how these conditions may act so as to produce the dwarfed phanerogamic vegetation and the abundance of cryptogams so characteristic of alpine districts.

The climatic conditions of our arctic-alpine regions may be considered directly, but it seems preferable to consider the arctic and the alpine conditions separately and then allow for the differences in our regions. General accounts of both arctic and alpine conditions are given by Schimper (15) and his account of alpine conditions, which seem to concern us most, must be carefully considered. Owing to the greater latitude of our alps and our insular position the influences of the various factors are considerably modified. The climatic conditions of alpine regions are largely consequent on the reduced atmospheric pressure. Owing to the tenuity of the air the absorption of the rays of the sun are reduced, the direct lighting and heating effects are more intense and there is a greater difference between sun and shade temperatures in alpine regions than in the lowlands. The soil is more strongly heated during sunshine and loses more heat, owing to the greater radiation, when sunshine is absent.

The relative humidity of the air is not necessarily greater or less than in the lowlands, but is more variable and more quickly variable, rapidly fluctuating between complete saturation and great dryness, any interception of the sun's rays causing a rapid lowering of temperature and raising the relative humidity. The condensation of water-vapour and its precipitation as rain are greater as the mountain is ascended, at any rate so far as the British mountains are concerned.

The movements of the air are more violent and continuous on the mountain than in the plain because the fluctuations of temperature are greater and more rapid.

The intense heating of the soil causes greater evaporation and the soil is occasionally very dry. At other times the alpine soil, especially in our islands, may be very wet owing to condensation of the water in the air, and this condensation may be copious, since, owing to air-movements, much of it is of water evaporated from the surface at lower levels.

During sunshine the temperature of the air will be lower than that of the soil because the latter absorbs heat better than the rarefied atmosphere. The conductivity of the soil is not sufficiently greater to neutralize this effect but sometimes the heat-energy may be expended in evaporating the water of a wet soil. The different levels of a plant 4 feet high will then be living in different zones of temperature, which may be very variable. The upper portion of the plant is, at times, living in a low temperature zone, whilst the subterranean portion may be in a zone with a much higher temperature. At one moment, when the sun's rays are intercepted, the top of the plant is actually living in the low temperature; at the next, it may have the benefit of direct heat from the sun. The conditions nearer the soil are more regular, the direct heating effects are usually slightly less. For one thing the absorptive power of the air is increased by the vapour from the soil and when shading occurs the temperature changes are less rapid owing to the heat-radiation from the warmer soil. It must also be remembered that the conditions near the surface will be

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rendered more stable by evaporation and condensation: during heating some of the energy is used for evaporation, during cooling some heat-energy will be liberated when condensation occurs. Besides, when the soil is wet it becomes hot or cold less quickly, owing to the greater specific heat of the contained water. It seems then that the less rapid variations in temperature of the plant-environment will be below but near the surface of the soil, at a level which will vary with the conditions, for instance, it will be different in soils of different textures. This relatively-constant stratum will be at a level where the rate of change due to various factors (direct heating, absorption, radiation, evaporation, condensation, conduction, etc.) is least rapid.

The xerophytic character of alpine phanerogamic vegetation has often been attributed to the incapacity of the root-system to absorb water owing to the low temperature. A study of the conditions renders this theoretically improbable. As the tissues most susceptible to injury by rapid changes are the actively-growing ones and as the zone with the most constant temperature is near the surface of the soil, it is not surprising that the most abundant alpine plants are of a low habit and that bryophytes and lichens contribute so largely to alpine vegetation. The active period is so much shortened in alpine or arctic regions that the reproductive phase must be of short duration, or, if of longer duration, be more resistant. The meristems of the sexual organs generally seem to be more resistant to cold than those of vegetative organs but many alpine plants depend largely on vegetative methods of reproduction. Sexual methods of reproduction are less necessary to the lower kinds of vegetation and when they occur do so more rapidly or have greater resistance than in the higher plants. The acceleration of the reproductive phase in flowering plants is one of the characteristic features of alpine vegetation. Flowering and fruiting must be accomplished quickly or the cold will ruin all, whereas in bryophytes and especially in lichens<sup>1</sup> the reproductive organs may not be ruined.

### UPPER ARCTIC-ALPINE FORMATIONS.

#### Formation of Mountain Top Detritus

##### *Moss-lichen Association.*

On the mountain summits exposed to extreme variations of temperature and humidity<sup>2</sup> bryophytes and lichens play an important part, and the community is well entitled to be called a moss-lichen association.

Many of the bryophytes and lichens of the moss-lichen association are strictly alpine, but it is surprising to find present in abundance a large number of plants which are common at much lower altitudes all over the country. As examples of such plants the following may be mentioned: *Polytrichum*

<sup>1</sup> The sexuality of these plants is a matter of dispute; it may have been lost.

<sup>2</sup> Variations in humidity are more extreme but are sometimes discounted by their more temporary character.

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*piliferum*, *Dicranum scoparium*, *Rhacomitrium canescens*, *Webera albicans*, *W. nutans*, *Bryum pseudotriquetrum*, *Brachythecium rutabulum*, *Hypnum cupressiforme*, *H. molluscum*, *H. schreberi*, *Plagiothecium denticulatum*, *Hylocomium splendens*, *Alicularia scalaris*, *Lophozia ventricosa*, *L. quinquedentata*, *L. floerkii*, *Cephalozia bicuspidata*, *Gymnocolea inflata*, *Diplophyllum albicans*, *Scapania irrigua*, *Cetraria aculeata*, *Peltigera polydactyla*, *P. canina*, *P. rufescens*, *Cladonia cervicornis*, *C. coccifera*, *C. squamosa*, *C. furcata*, *C. floerkeana* form *trachypoda*, *C. sylvatica*, *C. uncialis* and form *adunca*, *Lecidea uliginosa*, *L. contigua*, *L. crustulata* and *L. solediza*.

The members of the association are more or less xerophytic, but it must be noted that some of the plants, common to both the lowlands and the highlands, often show variations in structure from their lowland forms and some of these variations indicate that the species is living in a moister habitat than a typical plant from lowland districts. Both *Polytrichum piliferum* and *Rhacomitrium canescens*, when growing on a dry heath have their hair-points well developed but in forms from the arctic-alpine moss-lichen association the hair-points are often less conspicuous and in *R. canescens* may be almost absent. A similar variation is met with in this plant at lower altitudes when it grows in ditches. In *Diplophyllum albicans* the central line of hyaline cells is often obscure. Owing to their ability to absorb sufficient moisture by their whole surfaces some species, e.g. *Dichodontium pellucidum*, *Bryum pseudotriquetrum*, *Sphenolobus politus* (seldom found below 2000 ft.), *Scapania dentata*, *S. undulata*, which are usually found in more constantly wet situations at lower altitudes, are capable of existing.

*Plagiothecium denticulatum* and *Hypnum schreberi*, both of which flourish best in damp and somewhat shaded situations where variations in humidity are not large, have their xerophytic characters intensified. In *H. schreberi* the leaves are more concave, more obtuse and the margins more incurved than in the typical plant, and similar modifications are shown by *P. denticulatum* which differs so much from the type that the alpine plant is given a varietal status as *v. obtusifolium*.

The purplish covering caused by a terrestrial form of *Zygnema ericetorum* is sometimes very noticeable but is more frequent on peaty heaths at lower altitudes. *Salix herbacea* is sometimes infested with the parasitic fungus, *Rhytisma salicinum* (Ben Doran, 3000 feet), and parasitic fungi (such as *Ticothecium erraticum*) are often present on crustaceous lichens.

The nomenclature adopted in the following lists is usually that given by Dixon (7), Macvicar (12), and A. L. Smith (16).

The frequency of a plant is indicated as follows:

d. = dominant; a. = abundant; f. = frequent; o. = occasional; r. = rare; v.r. = very rare; l. = local.

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## *List of Moss-Lichen open association.*

On mountain detritus (stony ground of summits).

Alpine or arctic species are indicated by asterisks.

### *Mosses.*

- \**Polytrichum alpinum*, a.
- \**P. sexangulare*, l.a.
- P. piliferum*, a.
- P. juniperinum*, o.
- P. aloides*, o.
- P. commune*, o.
- Oligotrichum hercynicum*, a.
- Andreaea petrophila*, a.
- \*var. *alpestris* (rocks), o.
- A. crassinervia* (usu. on rock), f.
- \**A. alpina* (moister places), o.
- \**A. nivalis* (moister places), l.
- Blindia acuta*, f.
- \**Ditrichum zonatum*, f.
- \*var. *scabrifolium*
- Swartzia montana*, f.
- \*var. *compacta*, f.
- Ceratodon purpureus*, o.
- Dicranella heteromalla*, o.
- var. *interrupta*, o.
- Dichodontium pellucidum* (moist), o.
- \*var. *fagimontanum* (moist), o.
- Dicranum fuscescens*, a.
- \*var. *congestum*, f.
- D. scoparium*, o.
- var. *spadiceum*, o.
- D. starkei* (often on rock), o.
- D. falcatum*, l.f.
- D. schisti*, l.f.
- \**D. molle* (usu. on ledges), r.
- Dicranoweisia crispula*, l.f.
- Rhacomitrium lanuginosum*, a.
- R. heterostichum*, o.
- var. *gracilescens*, a.
- R. canescens*, o.
- Orthothecium rufescens*, o.
- \**Conostomum boreale*, f.
- \**Webera ludwigii* (moist), o.
- W. nutans*, a.
- W. elongata*, o.
- W. albicans* (moist), o.
- Oedipodium griffithianum* (usu. rock-nooks), o.
- Pterigynandrium filiforme*, o.
- Bryum pseudotriquetrum* (moist), o.
- \**Eurhynchium cirrosom*, r. and l.
- E. myosuroides*, o.
- E. swartzii*, o.
- \**Brachythecium glaciale*, r. and l.
- \**B. plicatum*, r. and l.
- B. rutabulum*, o.
- Plagiothecium elegans*, o.
- \**P. muhlenbeckii*, l.
- P. denticulatum*, f.
- var. *obtusifolium*, l.a.
- \**Hypnum hamulosum*, f.
- H. cupressiforme*, f.
- var. *ericetorum*, f.
- H. callichroum*, l.a.
- \**H. bambergeri*, o.
- H. molluscum*, l.f.
- \**H. procerrimum*, l. and r.
- H. schreberi*, l.a.
- \**H. revolutum*, r.
- H. incurvatum*, r.
- Hylocomium splendens*, a.
- H. loreum*, a.
- H. rugosum*, l.
- H. squarrosom*, o.
- H. triquetrum*, o.
- \**H. pyrenaicum*, l.

### *Liverworts.*

- \**Gymnomitrium obtusum*, o.
- \**G. corallioides*, o.
- \**G. concinnatum*, l.a.
- G. crenulatum*, o.
- \**G. varians*, l.a.
- \**G. crassifolium*, l.a.
- \**G. adustum*, o.
- \**G. alpinum*, o.
- \**Marsupella condensata*, l.a.
- \**M. ustulata*, o.
- Alicularia scalaris*, a.
- \**A. breidlerii*, l.f.
- Eucalyx subellipticus*, o.
- Plagiochila asplenioides*, f.
- var. *minor*, l.f.
- \**Pleurocladus albescentis*, l.f.
- Leptoscyphus taylori*, o.
- Lophozia ventricosa*, o.
- \**L. alpestris*, f.
- L. floerkii*, o.
- L. quinqueidentata*, o.
- L. incisa* (damp places), o.
- \**Sphenolobus politus*, o.
- \**Cephalozia ambigua*, l.
- C. bicuspidata*, f.
- Cephaloziella byssacea*, f.
- Gymnocolea inflata*, o.
- form *compacta* (drier places), o.
- form *laxa* (moist ground), o.
- \**Anthelia julacea*, a.
- \**A. juratzkana*, a.
- Bazzania tricrenata*, o.
- B. triangularis*, o.
- Diplophyllum albicans*, a.
- \**D. taxifolium*, r.
- Ptilidium ciliare*, f.
- Scapania irrigua* (small form), o.
- S. dentata* (moist places), o.
- S. undulata* (moist places), o.

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## Lichens.

- Collema tenax*, o.  
 \**C. ceraniscum*, r. and l.  
 \**Schizoma lichinodeum*, l.a.  
   *Leptogium lacerum*, o.  
     var. *pulvinatum*, o.  
 \**Placynthium delicatulum*, r.  
   *Peltidea aphthosa*, o.  
   *Peltigera canina* (small forms), o.  
   *P. rufescens*, o.  
   *P. polydactyla*, o.  
 \**Solorina crocea*, l.a.  
 \**S. bispora*, r.  
   *S. spongiosa*, r.  
   *Pannaria brunnea*, f.  
 \**P. hookeri*, l.  
 \**Parmeliella lepidota*, r.  
   *Sphaerophorus fragilis*, o.  
   *S. corallioides*, a.  
     form *congestus* (drier), a.  
 \**Alectoria sarmentosa*, r.  
   \*var. *cinninata*, r.  
 \**A. ochroleuca*, o.  
 \**A. divergens*, r.  
   *A. bicolor*, l.f.  
 \**Cetraria hiascens*, r.  
   *C. islandica*, a.  
     \*form *platyna*, o.  
   *C. crispa*, o.  
   *C. aculeata*, f.  
     var. *alpina*, o.  
 \**C. nivalis*, r.  
 \**C. cucullata*, r.  
 \**Platysma hepaticum*, l.a.  
 \**P. fahlunense*, o.  
 \**P. polyschizum*, o.  
   *Parmelia saxatilis*, o.  
 \**P. pubescens*, a.  
   \*var. *reticulata*  
 \**P. vittata*, r.  
 \**P. alpicola* (often on quartz), r.  
   *P. pristis* (usu. on rock), l.a.  
 \**Lecanora epibryon*, l.  
   *L. tartarea*, f.  
     \*var. *frigida*, l.a.  
     \*var. *gonatodes*  
       *L. subtartarea*, o.  
       *L. polytropia*, a.  
       *L. upsaliensis*, r.  
       *L. geminipara*, v.r.  
       *L. badia* (rocks), f.  
       *Haematomma ventosum* (rocks), l.a.  
 \**Lecania curvescens*, v.r.  
 \**Pertusaria oculata*, l.a.  
   *P. bryontha*, l.  
   *P. dactylina*, l.  
   *P. glomerata*, l.  
   *P. xanthostoma*, l.  
 \**Varicellaria microsticta*, l. and r.  
   *Gyrophora cylindrica*, a.  
   *G. polyphylla*, o.  
   *G. erosa* (rock), r.  
   *G. torrefracta* (rock), r.  
   *Icmadophila ericetorum*, o.  
   *Baeomyces rufus*, o.  
   *B. roseus*, o.  
   *Stereocaulon evolutum*, a.  
   *S. corallioides*, f.  
   *S. denudatum*, f.
- \**S. alpinum*, f.  
 \**S. tomentosum*, r.  
 \**Cerania vermicularis*, l.a.  
   *Cladonia uncialis*, a.  
     form *adunca*, a.  
     form *turgescens*, f.  
 \**C. destriata*, l.f.  
 \**C. amauroceras*, r.  
   *C. pyxidata*, o.  
   *C. degenerans*, o.  
     var. *phyllophora*, l.a.  
   *C. gracilescens*, l.f.  
   *C. gracilis*, l.a.  
   *C. verticillata*, o.  
   *C. gracilis*, f.  
   *C. cervicornis*, a.  
     var. *subcervicornis*, a.  
   *C. furcata*, a.  
     var. *pinnata*, a.  
   *C. crispata*, l.f.  
   *C. squamosa*, o.  
   *C. coccifera*, o.  
   *C. deformis*, o.  
   *C. flabelliformis*, o.  
   *C. floerkeana* f. *trachypoda*, l.a.  
 \**C. bellidiflora*, l.a.  
   *C. sylvatica*, f.  
   *C. rangiferina*  
 \**Gyalecta foveolaris*, o.  
 \**Lecidea rhizobola*, r.  
   *L. coarctata*, o.  
     var. *glebulosa*, o.  
     var. *elacista*, o.  
   *L. granulosa*, o.  
     \*var. *escharoides*, l.a.  
   *L. demissa*, f.  
 \**L. berengeriana*, l.  
   \*var. *lecanodes*  
     *L. uliginosa*, a.  
     *L. atrofusca* (on moss), o.  
     *L. aglaea*, o.  
   *L. limosa*, l.a.  
   *L. arctica*, l.a.  
   *L. alpestris*, l. and r.  
   *L. breadalbenensis*, r.  
     *L. sublatypha* (rock), o.  
   *L. nigroglomerata*, v.r.  
   *L. deparcula*, r.  
   *L. tabidula*, r.  
     *L. contigua*, f.  
       var. *flavicuuda*, f.  
       var. *platycarpa*, f.  
     *L. crustulata*, f.  
   *L. consentiens*, r.  
   *L. confluens*, f.  
   *L. sorediza*, o.  
   *L. lapicida*, o.  
   *L. lithophila*, o.  
   *L. fuscoatra*, o.  
   *L. kochiana*, o.  
   *L. griseoatra*, o.  
   *L. fuscocinerea*, l.  
   *L. auriculata*, l.f.  
     var. *diducens*  
   *L. pycnocarpa*, l.  
   *L. tessellata*, o.  
   *L. dicksonii*, l.f.
- } on rocks and stones

## 10 The Bryophytes and Lichens of Arctic-Alpine Vegetation

- |                            |                             |             |
|----------------------------|-----------------------------|-------------|
| *L. vernalis               | R. confervoides, l.a.       |             |
| L. epiphorbia, r.          | R. oederi, l.f.             |             |
| L. sanguinaria, o.         | *Buellia badioatratra, l.   | } on stones |
| *var. affinis              | *var. atrobadia, l.         |             |
| *Biatorella fossarum, l.   | *B. alpicola, l.            |             |
| *Biatorina cumulata, l.    | B. myriocarpa, o.           |             |
| *B. contristans, l.a.      | *B. puchella (rock-nooks)   |             |
| Bilimbia sabulosa          | Dermatocarpon hepaticum, o. |             |
| *var. montana              | D. lachneum, o.             |             |
| B. sabuletorum, o.         | D. cinereum, l.a.           |             |
| var. simplicior, r.        | *var. cartilagineum, l.f.   |             |
| B. lignaria, o.            | *Dacampia hookeri, l.a.     |             |
| B. melaena, l.a.           | *Polyblastia sendtneri, r.  |             |
| *B. rhexoblephara, l.      | *P. gelatinosa, r.          |             |
| Bacidia flavovirescens, o. | P. nigritella, r.           |             |
| *Rhizocarpon postumum, r.  | *Arthopyrenia bryospila, r. |             |
| R. geographicum, a.        | *Porina furvescens, r.      |             |
| var. atrovirens, o.        | *Thelopsis melathelia, r.   |             |
|                            |                             | } on stones |

### *Rhacomitrium* Heath.

The moss-lichen association is sometimes replaced by a closed association in which the woolly-fringe moss, *Rhacomitrium lanuginosum*, is often dominant. It often grades into the moss-lichen association and appears to be progressive from it. The phanerogams characteristic of the *Rhacomitrium* carpet are given in *Types* (18) but do not exclude those listed for the moss-lichen association. Wheldon gives *Empetrum nigrum* as abundant on the *Rhacomitrium* heath of Ben-y-Gloe (27) and Crampton and Macgregor give *Salix herbacea* and *Deschampia flexuosa* as abundant in the *Rhacomitrium* carpet of Ben Armine (5). These three plants are listed for the moss-lichen association only (18). A list of cryptogamic constituents of the *Rhacomitrium* heath, similarly, cannot be exclusive of those given for bordering associations. Hepatics are absent or rare in this association whereas lichens are abundant, especially if retrogression is occurring, in fact *Cladonias* may become co-dominant with *Rhacomitrium* and occasionally the latter becomes the subordinate partner on the plateau between Cader Idris and Mynwydd Moel. On some summits (e.g. Snowdon and the neighbouring mountains) the *Rhacomitrium* carpet consists chiefly of *R. heterostichum* var. *gracilescens* and approximates more to the moss-lichen heath. What may be called a *Rhacomitrium* heath is sometimes found at lower levels but the associated species are then different. Other associations or sub-associations are described by W. G. Smith (18) and by C. B. Crampton and M. Macgregor (5) for situations where peat has accumulated.

- |   |                                 |
|---|---------------------------------|
| <i>Rhacomitrium lanuginosum</i> , d.    | H. splendens, o.                |
| R. canescens var. ericoides, o.         | Ptilidium ciliare, o.           |
| R. heterostichum, v. gracilescens, l.a. | Leptoscyphus taylori, o.        |
| Dicranum fuscescens, o.                 | Cladonia sylvatica, a.          |
| D. uncinatum, r.                        | <sup>1</sup> C. rangiferina, a. |
| *Polytrichum alpinum, o.                | C. uncialis, a.                 |
| Hypnum schreberi, o.                    | form obtusata, a.               |
| H. cupressiforme, o.                    | form turgescens, a.             |
| Hylocomium loreum, o.                   | *C. stricta, l.                 |

<sup>1</sup> *C. sylvatica* and *C. rangiferina* are both recorded as abundant, but it is difficult to distinguish between our British examples so named.

<sup>1</sup> *C. cervicornis*, o.  
*C. gracilis*, o.  
*C. squamosa*, o.  
*C. furcata*, l.a.  
*C. degenerans*, o.  
     form *pleolepidea*, l.a.  
*C. deformis*, l.a.  
<sup>2</sup> *C. flabelliformis*, o.  
 \**C. bellidiflora*, o.  
*Icmadophila aeruginosa*, r.  
*Cetraria islandica*, l.a.

*C. aculeata*, o.  
*C. crispa*, l.a.  
     form *subnigrescens*, o.  
     \*var. *alpina*, o.  
*Alectoria nigricans*, l.a.  
 \**A. ochroleuca*, o.  
*Peltigera canina*, o.  
 \**Cerania vermicularis*, o.  
*Lecanora tartarea*, o.  
*Bilimbia melaena*, r.  
*Galera hypnorum*, r.

<sup>1</sup> Chiefly *C. subcervicornis* Wain.

<sup>2</sup> = *C. macilenta* v. *coronata* (Ach.) Nyl.

### Snow-patch Vegetation.

In some places the snow does not melt until late in the summer and thus special factors conditioning the growth of vegetation are introduced. The plants occurring in such habitats are able to withstand a low temperature though some heat is able to penetrate the snow, especially if it is pressed into a more or less icy mass. Any heat coming from the earth will also be prevented from escaping. The heat, whatever its source, will be used chiefly for liquefying the snow and any plants under the snow-patch will be at a temperature near the freezing-point. Such plants will be existing under more constant conditions than the plants which are not covered by the snow: the temperature will be constantly near the freezing-point and there will be a constant supply of cold water. Many plants are able to exist under such conditions and some can even thrive if sufficient light and air are able to enter. The most favourable habitat for some liverworts appears to be at the margin of the melting snow. *Pleuroclada albescens* is described in hepatic floras as having a white appearance, the leaves possessing little or no chlorophyll. The description has been taken from plants obtained from soil after the snow had melted and these plants were more or less moribund. Just underneath the snow-patch *Pleuroclada* is distinctly green and is in its most active condition. The Anthelias are similar in this respect, though they do not lose their chlorophyll so quickly, and may, under suitable conditions in regard to water and shade, preserve their chlorophyll long after the melting of the snow.

The presence of some other bryophytes in snow-patch vegetation may depend upon the accumulation of fine silt from the dust deposited on the surface of the snow.

The flowering plant which appears to be the most constant component of this vegetation is *Salix herbacea*. The following have also been recorded: *Cochlearia micacea*, *Saxifraga stellaris*, *Alchemilla alpina*, *Galium saxatile*, *Gnaphalium supinum*, *Azalea procumbens*, *Juncus triglumis*, *J. biglumis* and *Phleum alpinum* (18).

\**Polytrichum sexangulare* l.d.  
 \**P. alpinum* o.  
*Dicranum starkei* o.  
*D. schisti* o.  
*Oligotrichum hereynicum* l.a.  
*Rhacomitrium fasciculare* o.

\**Webera commutata* f.  
 \**W. cucullata* o.  
     *W. nutans* a.  
 \**Bryum arcticum* o.  
 \**B. mühlenbeckii*  
 \**Brachythecium plicatum* o.



## 12 *The Bryophytes and Lichens of Arctic-Alpine Vegetation*

\**B. glaciale* o.  
 \**Moerckia blytii* l.a.  
 \**Gymnomitrium alpinum* o.  
 \**G. adustum* o.  
 \**Marsupella ustulata* o.  
 \**M. condensata* l.a.  
 \**Pleuroclada albescens* l.d.  
 \**Anthelia julacea* a.  
 \**A. juratzkana* l.a.  
*Lophozia ventricosa* o.  
*Cephalozia bicuspidata* o.

*Diplophyllum albicans* a.  
*Scapania undulata* o.  
*Alicularia scalaris* a.  
*Alectoria bicolor*, o.  
 \**Cerania vermicularis*, l.a.  
*Cetraria islandica*, a.  
*C. crispa*, l.a.  
*C. aculeata*  
     \*var. *alpina*  
 \**Solorina bispora*  
 \**Lecidea consentiens*, l.a.

The *Marsupella* association of Macvicar (11, pp. 7-8) may be considered as a particular facies of snow-lie vegetation in which hepatics, especially those belonging to the genus *Marsupella*, are abundant. It extends further down the northern or eastern sides of a mountain than down the southern or western and especially where snow remains throughout part of the summer (11, p. 8). It is well shown on Ben Lawers. The species characteristic of this consociation are *Marsupella condensata* (a), *M. ustulata* (a), *Gymnomitrium varians* (a), *G. crassifolium* (a), *G. adustum*, *G. corallioides*, *G. concinnatum*, *Alicularia scalaris*, *A. breidleri*, *Anthelia juratzkana*, *A. julacea*, *Pleuroclada albescens*, *Diplophyllum albicans*, *D. taxifolium*, *Lophozia alpestris*, *L. ventricosa*, *L. floerkii*, *Ptilidium ciliare*, and *Dicranum falcatum*.

The *Anthelia* association of W. G. Smith (17) is equivalent to the snow-patch vegetation, or to Rübel's *Anthelietum* mentioned below. Rübel (14) for the Bernina region gives five association of snow hollows (*Schneetälchen*). Four (*Anthelietum*, *Polytrichetum*, *Salicetum herbaceae* and *Alchemilletum pentaphylleae*) of these occur on siliceous soil and the first three are represented in our islands. His fifth association is a *Salicetum reticulatae* on calcareous soil and this is not (or is at most poorly) represented in Scotland.

On two occasions I have been so fortunate as to find patches of snow still lying on the ground in the Highlands in the middle of August. At an altitude of over 3400 feet on Ben Lui the most conspicuous bryophyte at the margin of the melting snow was *Pleuroclada albescens*. It often formed almost pure masses but was sometimes intermixed with *Dicranum starkei*, *D. schisti*, *Oligotrichum hercynicum*, *Lophozia ventricosa*, *Cephalozia bicuspidata*, *Diplophyllum albicans*, and *Scapania undulata*. On Ben Doran, at an altitude of 3200 ft. *Moerckia blytii* was abundant and was actually forming capsules. *Gymnomitrium alpinum* (also forming capsules), *Alicularia scalaris*, *Polytrichum alpinum*, *Racomitrium fasciculare*, *Webera nutans* and *Salix herbacea* were also present, the *Salix* being abundant.

### ARCTIC-ALPINE CHOMOPHYTE FORMATION

The communities of the crags and corries are rich in bryophytes and lichens and slight differences in the conditioning factors are reflected in their diversity and constitution. The steepness of the surface, the quantity of soil, the amount and source of the water-supply, the degree of shade and so on, have indicative values to the expert collector as to the species likely to be

found there, though it is difficult to give a detailed and connected account of these subtle values within the limits of a paper. A gradual colonisation of the exposed rock-surfaces occurs and every gradation to the successive associations is displayed by the bryophytes and lichens, especially by the former. A talus vegetation in which *Allosurus crispus*, *Grimmia doniana*, *G. conferta*, *Seligeria recurvata*, *Gymnomitrium adustum*, *Lecidea dicksonii*, and *Verrucaria maculiformis* are prominent occurs but has only been investigated, in detail, at lower altitudes.

The first plants to find a footing on the bare rock are algae (cf. 8) and lichens, the former requiring a damper substratum than the latter in order to become noticeable constituents of the vegetation though *Trentepohlia* gives a reddish orange hue to many fairly dry rocks. The structure of some lichens renders them specially able to act as lithophytes. Collemoid lichens seldom occur except when the rocks are almost constantly damp and are rarely very dry or very wet. *Racodium* and *Coenogonium* seldom occur except on damp shady rocks. Crustaceous lichens are very abundant on dry rocks and those which are common are widely distributed species frequent at lower elevations, e.g. *Lecanora parella*, *L. tartarea*, *L. atra*, *L. polytropha*, *Lecidea contigua*, *L. solediza*, *L. crustulata*, *Rhizocarpon confervoides*, *R. geographicum*.

Crustaceous lichens which may be considered highland species are *Placodium elegans*, *Lecanora austera*, *L. frustulosa*, *Aspicilia alpina*, *A. chrysophana*, *A. leucophyma*, *A. pelobotrya*, *Acarospora admissa*, *Pertusaria gyrocheila*, *Lecidea fuscorubens*, *L. nigroglomerata*, *L. inserina*, *L. tabidula*, *L. phaeenterodes*, *L. tessellata*, *L. contiguella*, *L. umbonella*, *L. pycnocarpa*, *L. commaculans*, *Biatorina rhyphodiza*, *Buellia succedens*, *B. alpicola*, *B. deludens*, *B. badioatra*, *Rhizocarpon plicatilis*, *Polyblastia scotinospora*, *P. inumbrata*, but the altitudinal ranges of some of these have been insufficiently studied and the specific value is doubtful in some cases, e.g. *Lecidea fuscorubens* is considered by Th. Fries to be synonymous with *L. ochracea* which is not infrequent in lowland districts, and *Pertusaria gyrocheila* is considered by most lichenologists to be a form of *Lecanora tartarea*. Some useful information on the occurrence of these lichens is given by Wheldon (26).

A slight amount of erosion enables such lichens as *Dermatocarpon minutum* and species of *Gyrophora*, *Umbilicaria*, *Stereocaulon* and *Sphaerophorus* to establish themselves on exposed rock faces and these are accompanied or followed by mosses, species of *Andreae* and *Grimmia* being the earliest representatives, different species of the same genus varying in their powers of establishment. For example, the very rare moss, *Blinda caespititia* occurs in some of the small crevices, its near relative, *B. acuta*, being scattered over the face of the same rock. Some pleurocarpous mosses appear later and then phanerogamic chromophytes become well established in fissures or on rock ledges. In this succession hepatics are rare at first, gradually becoming more abundant till on ledges they often form the chief constituents. The converse is true of lichens,

*Exposed rock-faces.*

L is attached to the names of Lithophytes living on the surfaces of rocks or boulders in the earlier stages of erosion.

- \**Polytrichum alpinum*, o.  
*Andreaea petrophila*, f.  
   \*var. *alpestris*, L.  
   var. *acuminata*, L.  
 \**A. alpina*, L.  
   var. *compacta*, L.  
   *A. crassinervia*, L.  
   *A. rothii*, L.  
 \**A. nivalis*, L.  
*Ditrichum flexicaule*, o. (3250 ft., B. Eachan)  
*Swartzia montana*  
*Ceratodon purpureus*, o.  
 \**Cynodontium wahlenbergii*  
   *C. gracilescens*  
 \**C. virens*  
*Dichodontium pellucidum*, L. (moist)  
   \*var. *fagimontanum*, L.  
*Dicranella heteromalla*, o.  
 \**Blindia caespiticia*, L. (usually in little chinks  
   or crevices 3900 ft.)  
   *B. acuta*, L., a. (usually on moist faces, to  
   3900 ft.)  
*Dicranoweisia crispula* (c.fr. 2700 ft.)  
 \**Dicranum falcatum*, L.  
   *D. schisti*, L. (often in clefts)  
   *D. fuscescens*  
   \*var. *congestum*  
   *D. starkei* (often on stony ground)  
   *D. scoparium*  
   *D. longifolium*, L.  
 \**D. elongatum*, L.  
   *D. fulvellum*, L. (clefts)  
 \**Campylopus schwarzii*, L.  
*Fissidens osmundoides* (wet 3000 ft.)  
*Grimmia apocarpa*, L., f.  
   \*var. *alpicola*, L. (wet)  
   var. *pumila*, L.  
   var. *rivularis* (moist boulders)  
   *G. funalis*, L., f.  
   *G. doniana*, L.  
 \**G. alpestris*  
 \**G. unicolor*  
   *G. conferta*, L.  
   *G. torquata*, L.  
   *G. trichophylla*, L.  
 \**G. atrata* (wet)  
*Rhacomitrium lanuginosum*, o. (a. on ledges)  
*R. ramulosum* (often in almost pure tufts but  
   usually below 3200 ft.)  
*R. fasciculare*  
*R. heterostichum*, o.  
   var. *gracilescens*, f.  
*Trichostomum tortuosum* (3400 ft.)  
   \*var. *fragilifolium*  
 \**Encalypta commutata* (usu. in nooks, 3900 ft.)  
   \*var. *imberbis*  
   *E. rhabdocarpa*  
   *E. ciliata* (usu. on well eroded rock)  
*Anoetangium compactum*, f. (rocks often  
   a little shaded)  
*Zygodon lapponicus* (clefts)  
 \**Conostomum boreale* (often on ground but  
   not infrequent on rock)  
*Bartramia oederi* (usu. on well eroded  
   rocks)  
 \**Webera commutata*  
   *W. nutans* (usu. on soil-capped rocks)  
 \**Plagiobryum demissum*  
 \**Bryum arcticum* (3800 ft.)  
   *B. pseudotriquetrum*, o. on moist rocks  
   (usu. in wetter situations)  
*Mnium orthorrhynchum*  
 \**M. spinosum* (shaded)  
   *M. serratum*  
 \**M. lycopodioides* (shady)  
 \**Myurella julacea*  
 \**M. apiculata* (3250 ft.)  
*Pterigynandrium filiforme* (3000 ft.) sometimes  
   almost pure with a little *R. hetero-*  
   *stichum*, sometimes with *Grimmia*  
   *apocarpa* var. *pumila*  
 \**Pseudoleskea patens*  
 \**P. catenulata*  
 \**P. atrovirens*  
 \**P. striata* var. *saxicola*  
*Orthothecium rufescens* (3800 ft. damp)  
*Brachythecium glareosum* (3600 ft., B. Lawers)  
 \**B. plicatum* (sometimes among boulders,  
   3000 ft. B. Lawers)  
   *B. rutabulum*  
 \**B. glaciale*  
 \**Eurhynchium cirrosum*  
   *E. myosuroides* (3000 ft. B. Lawers)  
 \**Plagiothecium muhlenbeckii* (usu. on ground)  
*P. denticulatum* var. *obtusifolium* (usu. among  
   boulders)  
   *P. pulchellum* (usu. clefts)  
 \**Hypnum halleri* (3600 ft. B. Lawers)  
 \**H. revolutum*  
 \**H. procerrimum*  
 \**H. bambergeri* (occ. on rock, usu well-eroded,  
   or on detritus, 3900 B.L.)  
   *H. cupressiforme*  
 \**H. hamulosum*  
   *H. callichroum* (often on shady rocks)  
 \**H. sulcatum*, f. (3900 ft. B. Lawers, but rocks  
   are wet or moist)  
 \**Hylocomium pyrenaicum* (often among  
   boulders)

*Hypnum uncinatum*, *H. falcatum*, *H. revolvens*, and *H. schreberi* are also found on alpine rocks which are wet, or damp and shaded, or with a distinct soil-cap. *Hylocomium loreum*, *H. splendens*, *H. triquetrum*, *H. squarrosum*, and

*H. umbratum* also occur in the alpine region on rocks but only when they are shaded or a cap of soil exists.

Hepatics are rarely present on rocks unless they are wet, or shaded, or with a soil-cap, but they are often abundant on rocky ledges and may form conspicuous members of that association. *Gymnomitrium obtusum*, *Sphenolobus saxicolus*, *Chandonanthus setiformis* and *Radula lindbergii* var. *germana* are highland hepatics occurring on rocks in the early stages of erosion. *Frullania tamarisci*, owing to its possession of water-sacs (21), is also able to endure a similar habitat. The following hepatics may also occur on exposed rocks, though such a habitat is not a usual one for them. They flourish much better when the rock is moist or shaded or partly covered with a thin soil-cap.

\**Gymnomitrium concinnum*  
 \*var. *intermedium*  
 \**G. corallioides*  
*G. crenulatum*  
 \**G. alpinum*  
 \**Marsupella sparsifolia*  
*Alicularia scalaris*  
 \**Lophozia quadriloba*

*L. floerkii* (small form)  
*Plagiochila asplenioides* var. *minor*  
 \**Anthelia julacea*  
 \**A. juratzkana*  
*Herberta adunca*  
*Ptilidium ciliare*  
*Diplophyllum albicans*  
 \**D. taxifolium*

Many of these plants in this community are smaller or otherwise different from the typical plants. A specimen of *Lophozia floerkii* from Ben Lawers, at an altitude of 3800 feet, had the large underleaves and cilia at the bases of the leaf-lobes characteristic of the typical plant but its parts were smaller and its leaf-lobes were often two instead of three.

Lichens are abundant and the rocks and boulders often appear of a yellowish hue owing to the presence of *Rhizocarpon geographicum* (and the rarer *Buellia alpicola*), though this feature is not so noticeable as in the Swiss Alps. Most of the species listed are present in the earlier stages of erosion. Those from *Thermutis* to *Cetraria* (inclusive), the *Stereocaulons*, the *Cladonias* and a few others which are indicated otherwise, are not characteristic of rocks in their early eroded stages.

*Thermutis velutina* (damp), r.  
 \**Pyrenopsis haematopsis*  
 \**P. homoeopsis*  
*P. fuscata*  
 \**P. furfurea* (damp), r.  
 \**Euopsis granatina*  
*E. pulvinata* (damp)  
 \**Schizoma lichinodeum*, l.f.  
 \**Pterygium pannariellum*  
 \**Psorotichia furfurella*, r.  
*Ephebe lanata*, o.  
*E. hispidula*  
*Collema tenax*, o.  
 \**C. ceraniscum*, r.  
*C. multifidum*  
 form *marginale*  
*C. granuliferum*  
 \**Leptodium glebulentum* (moist)  
*L. rhyarodes* (wet rocks), l.f.

*Peltidea apthosa*  
*Peltigera canina*  
*P. rufescens*  
*P. polydactyla*  
 \**Solorina crocea*  
*Sphaerophorus compressus*  
*S. corallioides*, a.  
 form *congestus*, a.  
*Cetraria islandica* (usu. on ground), a.  
*C. aculeata* (usu. on ground), a.  
*C. odontella*  
*C. nivalis*, l.f.  
 \**Platysma hepaticum*, f.  
 \**P. fahlunense*  
 \**P. polyschizum*  
*Parmelia omphalodes*, f.  
 \**P. alpicola*  
 \**P. pubescens*, a.  
 \**P. encausta*, l.a.

- P. conspersa*, f.  
     var. *stenophylla*, l.a.  
 \**Squamaria chrysoleuca*, r.  
     *S. gelida*, f.  
 \**Placodium elegans*, o.  
 \**Callophisma siebenhaariana*, r.  
     *Haematomma ventosum*, a.  
     *Lecanora picea*, r.  
     *L. badia*, f.  
     *L. tartarea*, a.  
     *L. subtartarea*, a.  
 \**L. austera*, r.  
     *L. parella*, a.  
 \**L. frustulosa*  
     *L. polytropa*, a.  
     \*var. *alpigena*  
     *L. intricata*, f.  
     \*var. *leptacina*  
 \**Aspicilia alpina*, r.  
     *A. superiuscula*, r.  
 \**A. leucophyma*, r.  
     *A. cinerea*, o.  
 \**A. cinereorufescens*  
     \*form *diamarta* (moist), r.  
 \**A. pelobotrya*, r.  
 \**A. depressa*, o.  
     *A. gibbosa*, o.  
 \**A. chrysophana*, r.  
 \**Acarospora peliocypha*  
 \**A. admissa*  
     *A. discreta*  
     *Pertusaria lactea*  
     *P. dealbata*  
     *P. monogona*  
     *P. ceuthocarpa*  
     *P. concreta*  
     *Umbilicaria pustulata*  
 \**Gyrophora erosa*  
 \**G. torrefracta*  
 \**G. hyperborea*  
     *G. cylindrica*, a.  
     \*var. *delisei*  
 \**G. arctica*  
 \**G. leiocarpa*  
     *G. proboscoidea*  
     *G. polyphylla*  
     *G. polyrrhiza*  
 \**Stereocaulon alpinum*  
     *S. evolutum*  
     *Cladonia pyxidata*  
     *C. cervicornis*  
         form *stipata*, l.a.  
         var. *subcervicornis*, a.  
     *C. verticillata*  
     *C. furcata*  
     *C. squamosa*  
 \**C. bellidiflora*  
     *C. uncialis*  
     *C. sylvatica*  
     *C. rangiferina*  
     *Racodium rupestre* (damp)  
     *Coenogonium ebenum* (damp)  
     *Lecidea contigua*, a.  
         var. *platycarpa*  
         var. *flavicunda*, a.  
     *L. confluens*  
     *L. dealbatula*
- L. solediza*  
*L. crustulata*  
*L. cinerascens*  
*L. albocoerulescens*  
 \**L. deparcula*, r.  
 \**L. tabidula*, r.  
 \**L. tessellata*  
 \**L. nigroglomerata*  
     *L. sublatypea*  
     *L. plana*  
     *L. goniophila*  
     *L. lapicida*  
     *L. polycarpa*  
     *L. lithophila*  
     *L. auriculata*  
         var. *diducens*  
     *L. mesotropoides*, r.  
     *L. subkochiana*  
     *L. kochiana*  
 \**L. contiguella*  
     *L. leucophea*  
 \**L. pycnocarpa*  
 \**L. umbonella*  
 \**L. subgyratula*  
 \**L. armeniaca*  
     *L. fuscoatra*  
     *L. griseoatra*  
     *L. rivulosa*, l.a.  
     *L. dicksonii*, l.a.  
 \**L. commaculans*, r.  
     *L. sanguinaria*  
     *Biatorella simplex*, o.  
 \**Biatorina confusior*  
 \**B. cumulata*  
 \**B. rhytidiza*, r.  
 \**B. contristans*  
     *B. biformigera*  
     *B. candida*  
     *Bacidia flavovirescens*  
         \*var. *alpina*, o.  
 \**Buellia alpicola*, r.  
 \**B. deludens*, r.  
 \**B. badioatra*, r.  
     \*var. *atrobadia*, r.  
     *B. colludens*  
     *Rhizocarpon obscuratum*, o.  
     *R. geographicum*, a.  
     *R. confervoides*, a.  
     *R. oederi*, l.a.  
     *R. petreum*, l.a.  
 \**R. plicatilis*, r.  
 \**R. geminatum*, r.  
     *Coriscium viride* (usu. ledges)  
     *Dermatocarpon minutum*  
         var. *complicatum* (moister)  
     *D. hepaticum*  
     *Microthelia exerrans*  
     *Porina chlorotica*, o.  
     *Polyblastia theleodes*  
 \**P. scotinospora*  
     *P. fuscoargillacea*  
     *P. intercedens*  
     *Microglæna corrosa*  
         \*var. *nericensis*  
     *M. breadalbanensis*  
     *Thelidium papulare*, o.

*Rock Sedges.*

The bryophytic constituents are often very varied though sometimes pure masses of one species occur. Lichens and sphagna are rare, but foliose liverworts are generally abundant.

*Mosses.*

*Sphagnum acutifolium*, r.  
*S. molluscum*, o.  
*S. quinquefarium*, r.  
 \**Polytrichum alpinum*, o.  
*P. piliferum*  
*P. commune*  
*Oligotrichum hercynicum*  
*Andrea petrophila*  
 \**Campylopus schimperi*  
 \**Dicranum molle*, l.f.  
*D. fuscescens*, o.  
*D. scoparium*, o.  
*D. fulvellum*  
*Rhacomitrium lanuginosum*, a.—d.  
*R. fasciculare*  
*R. heterostichum*  
*Grimmia doniana*  
*Bartramia oederi*, o.  
*B. ithyphalla*, o.  
*Webera nutans*  
*W. elongata*  
*Bryum pseudotriquetrum*, f. (moist)  
*Mnium punctatum* (moist), l.f.  
     var. *elatum*, l.f.  
 \**M. spinosum*, o.  
*M. hornum*, o.  
*M. orthorrhynchum*

\**M. lycopodioides*  
*Oedipodium griffithianum*, f.  
 \**Myurella julacea*, o.  
 \**M. apiculata*, r.  
*Pterigynandrium filiforme*, o.  
*Heterocladium squarrosulum*  
 \**Pseudoleskea atrovirens*  
 \**Eurhynchium cirrosum*, l.f.  
*E. myosuroides*, o.  
*E. swartzii*, o.  
*Plagiothecium pulchellum*  
 \**P. muhlenbeckii*  
*P. denticulatum*  
     var. *obtusifolium*  
*P. elegans*  
 \**Hypnum halleri*  
*H. cupressiforme*  
 \**H. hamulosum*  
*H. callichroum*  
*H. molluscum*  
*H. schreberi*  
*Hylocomium loreum*, f.  
*H. splendens*, o.  
*H. triquetrum*, o.  
*H. squarrosum*, o.  
*H. rugosum*

*Hepatics.*

*Preissia quadrata*, o.  
*Reboulia hemispherica*, l.f.  
*Pellia neesiana*, o.  
*Alicularia scalaris*, l.f.  
*Metzgeria furcata*, o.  
 \**Gymnomitrium concinnum*  
*Marsupella emarginata*  
*Jamesoniella carringtonii*, l.f.  
*Anastrophyllum donianum*  
*Lophozia ventricosa*, o.  
*L. floerkii*, o.  
*L. quinqueidentata*, f.  
*L. incisa*, f.  
 \**L. lycopodioides*  
*L. hatcheri*  
 \**L. quadriloba*, r.  
 \**L. obtusa*, r.  
 \**L. heterocolpa*, r.  
*Anastrepta orcadensis*, l.f.  
 \**Sphenolobus politus*  
     \*var. *medelpadicus* r.

*Plagiochila asplenioides*, f.  
*Leptoscyphus taylori*, l.a.  
*Cephalozia bicuspidata* (moist), o.  
 \**C. pleniceps*  
*Bazzania tricenata*, f.  
*B. triangularis*  
*B. trilobata*  
*Blepharostoma trichophyllum* (moist), o.  
*Herberta adunca*, f.  
*H. hutchinsiae*, f.  
*Ptilidium ciliare*, o.  
*Diplophyllum albicans*, a.  
 \**D. taxifolium*, l. and r.  
*Scapania aequiloba*, o.  
 \**S. nimbosa*, r.  
*S. irrigua*, o.  
     \*var. *alpina*, r.  
 \**S. ornithopodioides*, o.  
*S. aspera*, o.  
*Pleurozia purpurea*, l.f.

*Lichens.*

\**Schizoma lichinodeum*, r.  
*Solorina saccata*, o.  
*Cetraria islandica*, l.f.  
*Sphaerophorus corallioides*, o.  
*Cladonia cervicornis*, o.  
     var. *stipata*, l.f.  
 \**Lecidea rubiformis*, r. and l.  
*L. lurida*, o.

*L. demissa*, o.  
*L. decipiens*, o.  
 \**L. cupreiformis*, r.  
*Biatorina candida*, o.  
 \**Buellia pulchella*, r.  
*Dermatocarpon lachneum*, o.  
*Coriscium viride*, o.

# the Bryophytes and Lichens of Arctic-Alpine Vegetation

## Association of shade chomophytes.

This is well shown in the ascent to Ben Lawers from the Killin side (above 3000 feet), in the hollows of block screes.

### Mosses.

- \*Polytrichum alpinum, f.
- Dicranum fuscescens, f.
- Racomitrium lanuginosum, f.
- R. canescens
- var. ericoides
- R. heterostichum, f.
- \*R. sudeticum
- Grimmia patens, f.
- Trichostomum tortuosum, o.
- Fissidens osmundioides, o.
- Anoetangium compactum, o.
- Webera elongata (also on mossy boulders)
- W. nutans
- W. annotina
- \*Timmia norvegica (moist place among rocks)
- Plagiobryum zierii
- \*Mnium spinosum, f.
- \*M. lycopodioides
- M. orthorrhynchum
- M. punctatum
- var. elatum (in well shaded or moist places among boulders)
- \*Pseudoleskea atrovirens, f.
- \*Brachythecium plicatum
- B. glareosum
- B. rutabulum
- Eurhynchium myosuroides
- E. swartzii
- E. praelongum,
- E. confertum (among boulders), f.
- Thuidium tamariscinum, o.
- \*T. philiberti v. pseudotamarisci
- Plagiothecium denticulatum, f.
- \*P. muhlenbeckii
- P. pulchellum
- Hypnum molluscum, a.
- H. callichroum, f.
- H. cupressiforme
- H. falcatum (in well-shaded or moist places among boulders)
- H. schreberi
- \*H. procerrimum
- Hylocomium umbratum, l.f.
- \*H. pyrenaicum, l.f.
- H. squarrosum
- H. loreum

The following are more usually found in small nooks of rocks:

- \*Saelania cesia
- P. aloides
- Ditrichum zonatum
- Dicranum fulvellum
- \*Grimmia elongata
- Rhabdoweisia fugax
- R. denticulata
- R. crenulata
- Oedipodium griffithianum
- Zygodon lapponicus
- Bartramia ithyphalla
- Myurella julacea

### Hepatics.

- \*Marchantia polymorpha v. alpestris, f.
- Preissia quadrata
- Aneura pinguis
- Pellia neesiana
- \*Gymnomitrium concinnatum
- \*var. intermedium
- Alicularia scalaris
- Lophozia ventricosa
- L. quinquedentata, f.
- \*L. lycopodioides
- L. hatcheri
- L. floerkii
- \*L. obtusa
- Plagiochila asplenoides
- var. minor, form laxa in damper places
- Anastrepta orcadensis
- Cephalozia bicuspidata
- Bazzania tricenata
- Diplophyllum albicans
- \*D. taxifolium
- Ptilidium ciliare
- Scapania dentata
- var. ambigua (in damper places)
- S. curta

These are associated with phanerogams such as *Cardamine flexuosa*, \**Alchemilla alpina*, *Oxalis acetosella* f., \**Saxifraga stellaris*, *Chrysosplenium oppositifolium* f., *Potentilla erecta* (form), *Adoxa moschatellina*, *Galium saxatile* f., \**Oxyria digyna*, \**Polygonum viviparum*, \**Polystichum lonchitis*.

Lichens are not characteristic of this association: Collembas such as *C. multifidum*, Peltigeras such as *P. canina*, *Racodium rupestre*, *Pannaria brunnea*, \**Solorina bispora*, *Peltidea aphthosa*, *Cladonia furcata*, and *C. sylvatica*, are occasionally found,

*Hydrophilous chomophytes.*

The association of hydrophilous chomophytes is rich in pleurocarpous mosses and many of these form plant-societies. The chief mosses forming societies are mentioned in the lists of plants. The constituents vary with the degree of submergence (cf. 5) and the aeration of the water, whilst other factors, such as the rapidity of the water and the amount of shading, have an influence on the vegetation. There are at least three facies: (a) moist rock surfaces, (b) ground and rock washed by spray, (c) aquatic communities (22). All of these may be shown on a boulder which projects above the water and the side which is more shaded or is more exposed to the current, supports a different vegetation from that supported by the other side (cf. 5).

The following are typical phanerogams: *Thalictrum alpinum*, *Cerastium alpinum*, *Chrysosplenium oppositifolium*, *Saxifraga stellaris*, *S. aizoides*, *Polygonum viviparum*, *Topfieldia palustris*, *Sagina saginoides*, *Equisetum hyemale*, *Carex saxatilis*, *Juncus triglumis*, *J. biglumis*.

Moss communities are often formed where spring water is in excess. There are several communities:

(a) *Philonotis* society in wet places where the water has a slow movement, and usually has little acidity.

(b) *Hypnum trifarium* on boggy wet slopes is locally a dominant moss. Other Hypna, such as *H. sarmentosum*, *H. revolvens*, *H. exannulatum* and *H. stramineum* are sometimes abundant with it.

(c) *Sphenolobus politus* is abundant in places similar to those of *Philonotis fontana* which may also be frequent. The water has more movement and its acidity is less.

(d) Marsupellas are dominant in places where the water flows over a substratum which is more or less rocky or stony. They usually form societies.

(e) Scapanias may form another association on somewhat boggy ground.

(f) Aplozias often form plant societies but are usually mixed. The following plants occur in such an association in the same boggy spring on Ben Lawers at an altitude of over 3000 feet: *A. cordifolia*, a., *A. riparia*, *A. atrovirens*, *Hypnum falcatum*, a., *H. revolvens*, a., *Bryum pseudotriquetrum*, a., *Sphagnum cymbifolium*, a., *Fissidens osmundoides*, o., *Alicularia scalaris*, f., *Aneura pinguis*, o., *Scapania undulata*, a., *S. dentata*, o., and *S. irrigua*.

The relationships of these consociations or societies to each other and to their environments are not definitely established.

The pleurocarpous mosses and the larger acrocarpous mosses are the chief mosses found in the hydrophilous chomophyte associations and include the following:

\**Polytrichum sexangulare*, wet ground, 3800 ft., B. Lawers, sometimes in pure patches (plant society).

\**P. alpinum* is a frequent invader of hydrophilous communities.

*P. commune*, a.

*Swartzia montana* (invader).



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\**Cynodontium virens* and \**C. wahlenbergii* often occur on wet and more or less stony ground, with *Fissidens adiantoides* and *Eucalyx obovatus*.

*Dichodontium pellucidum* usually occurs on rocks and sometimes on sandy detritus of springs; v. *compactum* in moist places with *Pellia neesiana* and *Hypnum stellatum*, also on wet ground with *Aplozia cordifolia* and *Bryum pseudotriquetrum*.

*Blindia acuta*, a. on wet faces of rocks.

*Dicranella squarrosa*, a.

\**Campylopus schimperi* occasionally occurs with *Mnium punctatum* but is rather a rock ledge plant.

*Fissidens osmundoides* usually on rocks, sometimes with *Aplozias* in springs

*Grimmia apocarpa* v. *rivularis* (moist boulders).

*Anoetangium compactum* is an occasional invader; v. *pellucidum* occurs in wetter places, usually on rocks.

\**Splachnum vasculosum*, in pools, springs and bogs.

*Meesia trichodes*, l.a., (boggy ground) sometimes forms societies but is usually intermixed with *Bryum pseudotriquetrum*, etc.

*Aulacomnium palustre*, f.

\**Taylora lingulata* occurs in boggy places with *Thalictrum alpinum*, *Equisetum hyemale*, *Hypnum revolvens*, *H. falcatum*, *Mnium punctatum* v. *elatum* and *Scapania dentata*; sometimes on wet ground as on Ben Lawers (3000 ft.) with *Lophozia quinquedentata*.

\**Timmia norvegica* is occasionally found with *Philonotis fontana* and *Hypnum revolvens* in moist places amongst rocks, but is rather a shade chomophyte.

*Philonotis fontana* often forms pure plant societies, but may be intermixed with *Hypna*, *Scapanias*, *Brya*, *Sphagna*, *Mnia*, etc.

*P. adpressa* (springs).

*P. calcarea* sometimes forms a plant society.

\**Webera ludwigii* (springs).

*W. elongata* is occasionally present but is an invader.

*W. albicans* (Ben Lawers, 3900 ft. moist soil); \*v. *glacialis* in pools, and on the sides of pools with *Philonotis fontana*.

*Bryum pallens* occurs in grassy and springy places.

*B. pseudotriquetrum* is often present with *Philonotis*, *Hypna*, *Scapanias* and *Aplozias*.

*B. alpinum* is sometimes present on wet rocks.

*Mnium cinclidioides* is a rare moss of pools and boggy places.

*M. punctatum* v. *elatum* a., in springs with *Sphenolobus politus* and *Hypnum sarmentosum*.

*M. subgobosum*.

*Cinclidium stygium* occurs in wet boggy places as on Ben Lawers (3000 ft.) with *Hypnum falcatum*, *H. decipiens* and *Bryum pseudotriquetrum*.

\**Thuidium philiberti* v. *pseudotamarisci* in moist places with *Polytrichum alpinum*.

*Cylindrothecium concinnum* (o) but not characteristic of this association.

*Orthothecium rufescens* usually on rocks but occasionally with *Scapanias*.

\**Hypnum decipiens* in a wet place on Ben Lawers (3500 ft.) is sometimes almost pure, but at other times is mixed with *Cinclidium stygium*, *Bryum pseudotriquetrum* and *H. falcatum*.

*H. stellatum*, o.

*H. lycopodioides*, o.

*H. fluitans*, o.

*H. exannulatum*, a.; v. *orthophyllum* in a boggy place (3200 ft.) Ben Doran, with *Dicranella squarrosa*, *Polytrichum commune*, *Hypnum sarmentosum* and *Scapania uliginosa*.

*H. vernicosum*, o., with *Scapanias* to 3000 ft. Ben Lui.

*H. revolvens*, a.

*H. commutatum*, a.

*H. falcatum*, a., often with *Cinclidium stygium* and *Bryum pseudotriquetrum*.

*H. uncinatum*.

\**H. molle*.

\**H. arcticum*.

*H. ochraceum* (Ben Doran, 3000 ft.).

*H. cuspidatum*.

*H. scorpioides*.

*H. stramineum*, a.

*H. trifarium*, l.a.

*H. sarmentosum*, f. to a., sometimes forming local societies.

*Hylocomium splendens*, *H. squarrosum*, *Hypnum molluscum*, *H. schreberi*, *Thuidium philiberti*, *Rhacomitrium lanuginosum*, *Lophozia incisa*, etc., are frequent invaders during times of drought.

Hepatics are abundant and characteristic of these associations.

*Aneura pinguis* is often present with *Sphenolobus politus*.

*Pellia epiphylla*, o.

*P. neesiana*, a., and replacing *P. epiphylla* at higher altitudes.

*Marsupella emarginata* usually occurs on moist rocks but sometimes on moist gritty soil.

*M. aquatica*, a., (society).

*M. pearsoni*, a., especially on dripping edges of rocks and banks forming a society.

*Alicularia scalaris*.

*Eucalyx obovatus*, o.

\**Aplozia sphaerocarpa* v. *nana*.

\**A. cordifolia*, a., (plant society).

*A. riparia*, f. to a. is often small and on rocks.

\**A. atrovirens* v. *sphaerocarpoidea* often occurs on rocks.

*Gymnocolea inflata*, o.; form *nigricans*, a., in boggy ground with *H. trifarium*.

*Lophozia muelleri* is rare except on rocks.

*L. bantriensis*, l.a. with *Sphenolobus politus*, etc.

\**L. wenzelii*, r. (wet ground).

\**L. lycopodioides*, f.

\**L. kunzeana*, r., in marshes, and on stream sides.

\**Sphenolobus politus*, a., in springs over 3000 ft. On Ben Doran it is associated with *Pellia neesiana*, *Scapania obliqua*, *Hypnum sarmentosum*, *Sphagnum inundatum* and *Harparanthus flotoicianus*, the last a common associate.

*Chiloscyphus polyanthus* v. *fragilis*.

\**Harparanthus flotoicianus*, l.f., is a common associate of *Sphenolobus politus*.

*Cephalozia bicuspidata*, a.

\**Eremonotus myriocarpus* usually occurs on wet rocks.

\**Hygrobiella laxifolia* usually occurs on wet rocks by stream sides.

*Blepharostoma trichophyllum*, o.

*Ptilidium ciliare*, o.

\**Anthelia julacea* v. *gracilis* on edges of ledges over which water trickles, often with reddish *Marsupella aquatica* and *Scapania dentata*.

*Scapania subalpina* on wet ground, especially by streams.

\**S. crassiretis* on wet rocks.

*S. dentata* and v. *ambigua*, a., in springs and on stones in water.

*S. undulata*, a., in springs and on stones in water.

*S. uliginosa*, a.

\**S. obliqua*, l.f.; in a spring at 3000 ft. on Ben Lui associated with *S. uliginosa*, *S. undulata*, *S. dentata*, *Fissidens adiantoides*, *Hypnum vernicosum*, *Bryum pseudotriquetrum* and *Aulacomnium palustre*.

\**S. paludosa*, r., in marshes.

*S. irrigua* in springs at 3000 ft. with *S. dentata* and *S. uliginosa*.

Lichens are seldom present, but the following may occur on stones in streams, or on wet rocks by stream-sides: \**Pyrenopsis phylliscella*, *Ephebe hispidula*, *E. pubescens*, \**Psorotichia furfurella* (often with *E. pubescens*), *Collemodium fluviatile*, *Aspicilia lacustris*, *Lecidea contigua* f. *hydrophila*, *Verrucaria submersa*, *V. laevata*, *V. margacea*, *V. aethiobola*, *Polyblastia theleodes*, \**P. inumbrata*, *Staurothelè clopima*, and *Dermatocarpon miniatum* v. *complicatum*.

My thanks are due to Messrs Dixon, Duncan Jones (D. A.), and Knight for help in the field-work and also in regard to some of the data for the table of altitudinal distribution. I am also indebted to Mr Tansley for help during the preparation of the manuscript.

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### ALTITUDINAL DISTRIBUTION OF BRYOPHYTES AND LICHENS.

The approximate ranges of some of the bryophytes and lichens which occur in the arctic-alpine regions of the British Isles are shown in the following tables. The zone of greatest frequency is indicated by a continuous line. Extension of the range in the British Isles is shown by dots. Where the dots are further apart the plant is uncommon, so far as records indicate, for those altitudes.

The distributions of some plants given in the list are better known on the continental Alps. The supposed absence or rarity on our mountains of some cryptogamic plants, which are frequent on the Alps, may be due in some cases to lack of suitable habitats, but is often due to insufficient data. For such plants the probable extensions of their ranges are indicated by commas or discontinuous lines, the latter being used when the plants are frequent at equivalent altitudes on the Alps. In such cases the data given are approximations only since allowances must be made for differences of conditions, etc. All the heights are approximately corrected for the latitude of Perthshire by means of an empirical formula and graph.

	Fect 0	1000	2000	3000	4000	4400
Mosses	Metres 1	305	610	914	1219	1341
<i>Andrea nivalis</i>				.....		
<i>A. petrophila</i>		.....				
<i>A. crassinervia</i>		.....				
<i>Oligotrichum hercynicum</i>		.....				
<i>Polytrichum sexangulare</i>				.....		
<i>P. alpinum</i>		.....				
<i>P. piliferum</i>		.....				
<i>Ditrichum zonatum</i>			.....			
<i>Ceratodon purpureus</i>		.....				
<i>Blindia caespiticia</i>					.....	
<i>B. acuta</i>		.....				
<i>Dicranum molle</i>				.....		
<i>D. scoparium</i>		.....				
<i>D. fuscescens</i>		.....				
<i>D. starkei</i>				.....		
<i>Rhacomitrium ramulosum</i>			.....			
<i>R. heterostichum</i> (and vars.)		.....				
<i>R. lanuginosum</i>		.....				
<i>Trichostomum tortuosum</i>		.....				
<i>Oedipodium griffithianum</i>				.....		
<i>Conostomum boreale</i>				.....		
<i>Timmia norvegica</i>				.....		
<i>Philonotis fontana</i>		.....				
<i>Webera ludwigii</i>			.....			
<i>W. nutans</i>		.....				
<i>W. commutata</i>				.....		
<i>Bryum arcticum</i>		.....				
<i>B. alpinum</i>		.....				
<i>B. pseudotriquetrum</i>		.....				
<i>B. capillare</i>		.....				
<i>B. mühlenbeckii</i>			.....			
<i>Mnium serratum</i>			.....			
<i>M. hornum</i>		.....				
<i>Pseudoleskea atrovirens</i>			.....			
<i>Myurella apiculata</i>				.....		

	Feet 0	1000	2000	3000	4000	4400
MOSSSES (cont.)	Metres 0	305	610	914	1219	1341
<i>Brachythecium glaciale</i>				.....		
<i>B. plicatum</i>				.....		
<i>B. rutabulum</i>				.....		
<i>Orthothecium rufescens</i>		.....				
<i>Plagiothecium denticulatum</i>		.....				
<i>Hypnum halleri</i>				.....		
<i>H. cupressiforme</i>				.....		
<i>H. hamulosum</i>			.....			
<i>H. bambergeri</i>				.....		
<i>H. callichroum</i>		.....				
<i>H. molluseum</i>		.....				
<i>H. revolutum</i>					.....	
<i>H. schreberi</i>					.....	
<i>H. exannulatum</i>					.....	
<i>Eurhynchium cirrosum</i>				.....		
<i>E. myosuroides</i>				.....		
<i>Hylocomium pyrenaicum</i>				.....		
<i>H. splendens</i>					.....	
<i>H. loreum</i>				.....		

## HEPATICIS

<i>Conocephalum conicum</i>	.....					
<i>Preissia quadrata</i>	.....					
<i>Marchantia polymorpha</i> var. <i>alpestris</i>	.....					
<i>Aneura pinguis</i>	.....				.....	
<i>A. multifida</i>	.....					
<i>Moerkia blytii</i>	.....				.....	
<i>Pellia epiphylla</i>	.....					
<i>P. neesiana</i>	.....				.....	
<i>Marsupella condensata</i>	.....				.....	
<i>M. apiculata</i>	.....				.....	
<i>M. stableri</i>	.....					
<i>M. ustulata</i>	.....					
<i>M. nevicensis</i>	.....				.....	
<i>M. emarginata</i>	.....				.....	
<i>M. sullivantii</i>	.....				.....	
<i>M. pearsoni</i>	.....				.....	
<i>M. aquatica</i>	.....					
<i>Gymnomitrium varians</i>	.....					
<i>G. concinnum</i>	.....					
<i>G. crassifolium</i>	.....					
<i>G. obtusum</i>	.....					
<i>G. corallioides</i>	.....					
<i>G. crenulatum</i>	.....					
<i>G. adustum</i>	.....					
<i>G. alpinum</i>	.....					
<i>Alicularia breidlerii</i>	.....					
<i>A. scalaris</i>	.....					
<i>Eucalyx subellipticus</i>	.....				.....	
<i>E. obovatus</i>	.....				.....	
<i>Aplozia cordifolia</i>	.....				.....	
<i>Anastrophyllum donianum</i>	.....					
<i>Gymnocolea inflata</i>	.....					
<i>Lophozia alpestris</i>	.....					
<i>L. ventricosa</i>	.....					
<i>L. incisa</i>	.....				.....	
<i>L. quinqueidentata</i>	.....				.....	
<i>L. lycopodioides</i>	.....					
<i>L. floerkii</i>	.....				.....	
<i>L. quadriloba</i>	.....					
<i>L. kunzeana</i>	.....					
<i>Sphenolobus politus</i>	.....					
<i>S. minutus</i>	.....				.....	
<i>Plagiochila asplenoides</i>	.....				.....	

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	Feet	0	1000	2000	3000	4000
	Metres	0	305	610	914	1219
HEPATICS (cont.)						
Harpanthus flotowianus						
Cephalozia bicuspidata						
Cephaloziella byssacea						
Eremonotus myriocarpus						
Hygrobiella laxifolia						
Pleuroclada albescens						
Odontoschisma macounii						
Calypogeia trichomanis						
Blepharostoma trichophyllum						
Bazzania trierenata						
B. triangularis						
Anthelia julacca						
A. juratzkana						
Ptilidium ciliare						
Diplophyllum albicans						
D. taxifolium						
Scapania subalpina						
S. dentata						
S. undulata						
S. uliginosa						
S. irrigua						
S. gracilis						
Radula lindbergii var. germana						
LICHENS						
Collema ceraniscum						
C. tenax						
C. multifidum						
Leptogium pulvinatum						
Peltidea aphthosa						
Solorina crocea						
S. bispora						
Peltigera rufescens						
Pannaria brunnea						
Sphaerophorus coralloides						
Alectoria nigricans						
A. bicolor						
Cetraria islandica						
C. aculeata						
Platysma nivale						
P. hepaticum						
Parmelia saxatilis						
P. pubescens						
P. tristis						
Placodium elegans						
Lecanora polytricha						
L. intricata						
L. badia						
L. atra						
L. tartarea						
L. subtartarea						
Haematomma ventosum						
Aspicilia cinerea						
A. gibbosa						
Acarospora discreta						
Biatorella simplex						
Pertusaria oculata						
P. dealbata						
Gyrophora cylindrica						
G. torrefracta						
Cerania vermicularis						
Stereocaulon coralloides						
S. denudatum						
Cladonia sylvatica						

	Feet 0	1000	2000	3000	4000	440
	Metres 1	305	610	914	1219	134
LICHENS ( <i>cont.</i> )						
<i>C. amaurocrea</i>						
<i>C. destriata</i>						
<i>C. pyxidata</i>						
<i>C. fimbriata</i>						
<i>C. degenerans</i>						
<i>C. cervicornis</i>						
<i>C. verticillata</i>						
<i>C. gracilis</i>						
<i>C. furcata</i>						
<i>C. crispata</i>						
<i>C. squamosa</i>						
<i>C. uncialis</i>						
<i>C. bellidiflora</i>						
<i>C. deformis</i>						
<i>C. coccifera</i>						
<i>Lecidea decipiens</i>						
<i>L. lurida</i>						
<i>L. coarctata</i>						
<i>L. granulosa</i>						
<i>L. demissa</i>						
<i>L. uliginosa</i>						
<i>L. leucophea</i>						
<i>L. limosa</i>						
<i>L. alpestris</i>						
<i>L. contigua</i>						
<i>L. sorediza</i>						
<i>L. albocerulescens</i>						
<i>L. confluens</i>						
<i>L. cinerascens</i>						
<i>L. lapicida</i>						
<i>L. dicksonii</i>						
<i>Biatorina candida</i>						
<i>B. cumulata</i>						
<i>B. contristans</i>						
<i>Bilimbia lignaria</i>						
<i>Bacidia flavovirescens</i>						
<i>Buellia colludens</i>						
<i>B. badioatra</i>						
<i>B. alpicola</i>						
<i>Rhizocarpon geographicum</i>						
<i>R. oederi</i>						
<i>R. confervoides</i>						
<i>R. postumum</i>						
<i>R. obscuratum</i>						
<i>Lopadium pezizoides</i>						
<i>Arthonia lapidicola</i>						
<i>Lithographa tesserata</i>						
<i>Coriscium viride</i>						
<i>Dermatocarpon hepaticum</i>						
<i>D. cinereum</i>						
<i>Thelidium pyrenophorum</i>						
<i>T. papulare</i>						
<i>Polyblastia intercedens</i>						
<i>P. gelatinosa</i>						
<i>P. theleodes</i>						
<i>Microglena corrosa</i>						
<i>Theleopsis melathelia</i>						
<i>Porina chlorotica</i>						

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# THE ECOLOGY OF BRITISH BEECHWOODS WITH SPECIAL REFERENCE TO THEIR REGENERATION

## PART II, SECTIONS II AND III<sup>1</sup>.

### THE DEVELOPMENT AND STRUCTURE OF BEECH COMMUNITIES ON THE SUSSEX DOWNS (*continued*).

BY A. S. WATT.

(*With four Figures in the Text.*)

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#### SECTION 2.

##### THE REPRODUCTION OF BEECH COMMUNITIES.

The passage from the beech associates to the beech consociation is essentially a development within the quasi-organism and the key to the structure of the climax community is found in a study of the *modus operandi* of beech reproduction. Since this latter is similar in the associates and the consociation the following treatment applies to both. The difficulties attendant upon beech regeneration have been dealt with in Part I, yet natural woods descended from pre-existing beechwoods do occur as can be testified by the local inhabitants and woods in all stages of their development may be seen on the S. Downs.

<sup>1</sup> Part I appeared in this JOURNAL 11 (1923), p. 1 and Part II, Section I, in 12 (1924), p. 145.



Prior to a description of the *modus operandi* of successful beech reproduction a few preliminary considerations will be dealt with.

#### SEED PRODUCTION.

Continental authors seem agreed as to the age at which beech first produces seed. Klein<sup>1</sup>, Mathieu<sup>2</sup>, and Hempel and Wilhelm<sup>3</sup> state that seed-bearing begins in the 40th-50th year in the open, "but seldom before the 60th year and often first in the 80th year in close canopy" (Klein).

From the same sources we find that there is agreement in the main about the periodicity of seed production, although there is a considerable latitude regarding the duration of the intervals between seed years. Under favourable conditions good mast years occur every 5-8 years (Klein), 5-6 years (Mathieu) and 5-8 years (Hempel and Wilhelm) whilst good seed years may be separated by longer intervals, e.g. 15-20 (Mathieu) and 9-12 years (Klein, and Hempel and Wilhelm). It is pointed out, however, that between the full mast years partial crops occur, and that the frequency of production varies with altitude. "Full crops are generally more common on the plains and on low hills (*coteaux*) than on the mountains: but there the years of absolute lack are not rare whilst on the mountains partial crops succeed each other almost without interruption<sup>4</sup>."

Since 1890, the following full mast years have been recorded in this country.

1890	General?	Elwes and Henry, vol. 1, p. 14.
1900	South of England	Forbes, <i>Eng. Arb. Soc. Trans.</i> 1902-3, p. 267.
1906	Sussex	Local testimony.
1907	Bucks	Mr Hobart-Hampden.
1909	Bucks and Sussex	Mr Hobart-Hampden and Mr Cave in litt.
1920	N.E. Scotland	
1922	General	

Since 1912 partial crops have occurred in the following years on the S. Downs: 1912, 1915, 1917, 1918, 1919, 1920. For reasons given in Part I the offspring of these partial crops disappear so that the successful young growth dates from a full mast year. On the S. Downs successful regeneration can be referred to the years 1890, 1900 and 1906. Thus the limitation of effective regeneration to the full mast years, separated by intervals of varying duration, determines the even-aged character of the young wood.

We thus see that the production of heavy crops of mast occurs at irregular intervals and is not necessarily uniform throughout the beech area at the same date. For example, in 1920 a full mast crop was produced in N.E. Scotland, whilst in Sussex the crop was only partial. In 1918 a partial crop in Sussex was paralleled by an abundant crop in the Forêt de Compiègne and in Kanton Schaffhausen<sup>5</sup>. This suggests a possible relation to variation in weather in the different localities.

<sup>1</sup> In Lorey's *Forstwissenschaft und Forstwirtschaft*, 1913, p. 433.

<sup>2</sup> *Flore forestière*, 1897, p. 318.

<sup>3</sup> *Die Bäume und Sträucher des Waldes*, Part II, p. 42.

<sup>4</sup> Jolyet, *Traité de Silviculture*, 1916, p. 128.

<sup>5</sup> *Bot. Abstracts*, 1921, Nos. 773 and 952.

Although mast production may be general over an area, it does not necessarily follow that all trees of seed-bearing age produce seed. The year 1922 is recognised as a year of heavy mast production yet (at Easter 1923) on the Downs seedlings were local. Whilst isolated and marginal trees often covered the ground beneath carpeted with seedlings, this was not invariably so. Further within the associates and consociation the occurrence of seedlings was very local, and whilst gaps and rides in the woods generally showed seedlings, many were entirely devoid of them and under the general canopy of the beech consociation seedlings were recorded as rare. Yet on certain steep calcareous slopes and sometimes in damp bottoms seedlings were abundant. From the observations made no general correlation could be established between seed production and soil factors.

Again trees in the open may bear a good crop of mast whilst trees in close canopy bear none, so that the fruitfulness of an isolated tree is no index of seed production in a forest. Further even isolated trees vary much in their productivity, some bearing mast while adjoining trees show none. Sometimes the fruitfulness is only apparent and the "seeds" produced are only empty husks.

No definite information has been obtained regarding the productivity of beech and the age of the tree, but practical foresters consider that trees from 80-120 years of age are best for seeding purposes.

The causes of the periodicity of mast production are obscure but as already mentioned some correlation between mast production and weather is indicated. Of the climatic factors data regarding rainfall are available for a period of years, and the following comparisons with the average may be correlated with mast production<sup>1</sup>.

Table showing percentage excess or deficit of rainfall above or below the average for West Sussex in each of the years 1887 to 1922. The years printed in heavy type are those of heavy fertile mast production.

Average annual rainfall (W. Sussex) = 35.88 ins. (1887-1922).

Per cent.		Per cent.		Per cent.	
1887	-20.45	1899	-12.62	1911	+5.88
1888	+6.63	<b>1900</b>	+5.52	1912	+22.41
1889	-6.85	1901	-14.55	1913	+5.91
<b>1890</b>	-13.04	1902	-9.70	1914	+14.27
1891	+24.77	1903	+34.52	1915	+30.21
1892	-18.25	1904	-2.20	1916	+6.60
1893	-22.60	1905	-18.25	1917	-7.08
1894	+17.97	<b>1906</b>	+10.98	1918	-4.93
1895	-3.150	1907	+1.03	1919	+9.53
1896	-1.12	1908	-7.97	1920	+4.18
1897	-1.37	<b>1909</b>	+15.58	1921	-43.30
1898	-20.73	1910	+7.47	<b>1922</b>	+3.07

The above data show that a mast year has been invariably preceded by a year with a rainfall less than the average although the converse is not true. The failure to produce fertile mast in every year following one of deficient

<sup>1</sup> In West Sussex continuous records from 1887 to 1922 are available from Chilgrove and Compton and, with the exception of data for one year, from West Dean.

rainfall may be due to some other factor such as late spring frosts. Whether the low rainfall or the frequently accompanying large number of hours of sunshine or some other related factor is responsible for inducing flower and fruit production has not been determined, but the above data suggest some direct or indirect connection between rainfall and the productivity of mast. In connection with the above Mr Tansley suggests that the ability of the beech to produce ripe mast may decrease with the westward occurrence of this tree and this may act as a factor in retarding the rate of the natural migration of beech in an oceanic climate. No data by which this suggestion might be tested appear to be available.

#### FRUIT DISPERSAL.

Beech is a heavy seeded tree whose fruit has no special means of securing dispersal. Smaller and less heavy than the acorn and hazel-nut, it yet does not appear to travel so far—if the occurrence of young beech outside the wood can be relied upon to give a true measure of seed dispersal. Since, however, young oaks have a much better recuperative power than beech, the latter would be considerably handicapped compared with the former in colonising grazed areas and too much reliance cannot be placed on this observation as giving a true index of their relative capacities to migrate. Nothing is more striking than the local frequency of young oaks colonising the grassland adjoining the beech associates and the comparative infrequency of the beech. The acorn, however, is known to be carried long distances by birds, and owing to its size the carriers would have to alight in order to eat it. Unconsumed portions (sufficient to produce a seedling) may be left behind. Again the acorn is round in section and may be more liable to slip from its carrier's beak. But whatever the reason it is certain that seedling oaks appear at long distances from the nearest parent trees. Compared with the acorn the beech nut is smaller and tetrahedral in outline, and by wood pigeons at least the nut is consumed whole, obviating the necessity of alighting on the ground. Among quadrupeds the animals most likely to act as agents of dispersal are squirrels, mice and rats. Squirrels bury nuts where they find them and the forgotten nut may germinate and a young plant become established. Mice store beech nuts but are not likely to carry them long distances. Young beech at a distance of 100 yards or more from the nearest parents do occur, but nothing definite is known as to the agent of dispersal, although in all probability birds are responsible.

Beech mast has no adaptation for wind dispersal, yet the migration of beech in bulk seems to depend largely on the ability of the wind to carry the seed. In the case of isolated trees and trees occurring as marginal constituents of narrow shelter belts where the velocity of the wind is little interfered with, beech mast after a hurricane was found 35 yards from the vertical projection of the crown of a 70 ft. tall beech, while empty pericarps were

found 11 yards further on. Seeds carried this distance, however, had an average weight of only .198 gm. whilst the weight of a normal freshly collected nut is on the average .35-.40 gm. In answer to a question on this point Mr A. C. Forbes writes: "The seedling growing furthest from the parent trees is at 40 yards, measuring from the branch spread of the nearest tree, and to the east of it. Seedlings are quite numerous for a space of 20 yards from parent trees but become scarcer after that space. Of course I have no witness to show whether the seedlings are from wind blown seed or from that carried by birds, mice, rats, etc., but the presumption is that they were carried by wind" (in litt. 1921). The seedlings referred to occurred on land previously under cultivation and surrounded on three sides by beech trees 80 ft. high. In a later communication Mr Forbes writes: "I came across two seedlings germinating last spring about 300 yards from the nearest tree. How these were carried I could not ascertain but possibly by pigeons" (in litt. Nov. 1923). Generally seed may not be carried so far and local opinion on the Downs puts the general maximum distance of wind transported seed at about 20 yards.

While the above is applicable to isolated and marginal trees it does not seem to hold good of a closed canopy, where the efficacy of the wind is reduced.

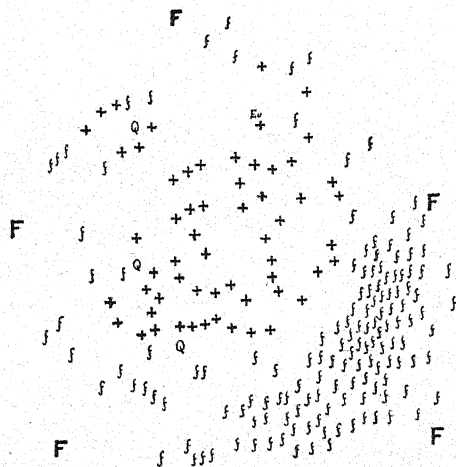


FIG. 1. Reproduction Circle of Beech. Gap in beech associates (sere 2) showing young ash in the centre and peripheral zone of young beech. Young beech dates from 1906. (For symbols v. Fig. 2, p. 32.)

Thus if a gap is made in a wood by the fall of a tree few seedlings are found much beyond the vertical projection of the crowns of the trees bordering the gap. Under these circumstances, that is to say, mast falls almost vertically downwards and little falls outside the area covered by the crown. Thus the central portion of the gap is not provided with seed, if the break in the canopy is more than about 6 ft. in diameter. Departures from this occur and the distribution of nuts within the gap will depend upon the effect of the wind and its

direction when the nut is ripe. Thus on west-facing and exposed slopes a gap would tend to be more evenly seeded than one formed in a wood sheltered from the S.W. winds and the reverse would happen if the time of ripening coincided with winds from the N.E. Nevertheless, in woods on plateaux the zone of maximum seeding does not extend beyond the vertical projection of the crown (v. Figs. 1 and 2).

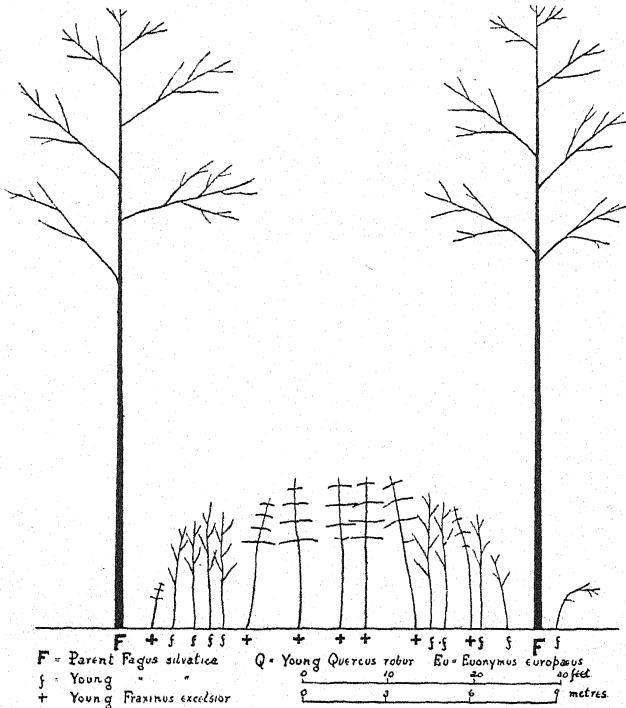


FIG. 2. Semi-diagrammatic section of Fig. 1 showing the taller ash in the centre with beech peripheral and suppressed beech and ash under canopy.

#### THE ESTABLISHMENT OF REGENERATING BEECH.

The fate of the nut has already been discussed<sup>1</sup> and evidence adduced to show that the crop of a poor mast year may be almost entirely consumed by animals, but that during a good mast year a sufficient quantity is left to stock the ground adequately with seedlings.

The study of the relation of beech seedlings to animals gives conclusions similar to those obtained for nuts, viz.: that when seedlings are abundant a large number escape the attentions of animals, vertebrate and invertebrate, or are only affected to an extent insufficient to cause serious crippling or death. Hence the seedlings that come up after a partial crop are heavily handicapped and in time disappear. Apart from those agents which directly reduce the assimilative surface particular reference has been made to those leaf-sucking

<sup>1</sup> Part I, this JOURNAL, 11, 1923, p. 2.

insects which reduce the seedling's capacity to bear shade. Consequently, under the prevailing conditions seedling beech demands a quantity of light in excess of the minimum necessary for survival when inhibiting factors are not present. Thus young beech cannot form an undergrowth under a beech canopy permitting the dominance of *Oxalis acetosella* or *Rubus fruticosus* (agg.), where attacked seedlings die or are severely crippled by shade. In this way normal growth of regenerating beech is to be found almost entirely in gaps. During 1921 it was practically impossible to obtain a living seedling under a canopy permitting the dominance of *Oxalis*, yet a few were to be found in the gaps. From the environs of a gap, therefore, seedlings disappear and only those present at the periphery of the gap itself survive and grow normally—the immobility of the seed preventing normal seeding of the centre of the gap. Thus there grows up a circle of young beech enclosing a central area for the most part devoid of beech (v. Figs. 1 and 2).

The most successful examples of beech regeneration were observed in the beech associates, although the primordia of such were found in the *Oxalis* and *Rubus* stages of the consociation (sere 2)<sup>1</sup>. In order to understand the *modus operandi* of beech regeneration it will be necessary to study these gaps more in detail. In the first place attention may be called to the great variation in their floras. The following lists (v. pp. 33 and 34) are representative of the plants found in gaps formed during the *Oxalis* and *Rubus* stages of consociation—sere 2 and in the beechwood associates.

*Flora of Gaps formed in the Beech Associates (sere 2) and during the Oxalis and Rubus stages of Consociation (sere 2).*

Woody Plants.	Beech Associates (sere 2)	Consociation (sere 2)	
		<i>Oxalis</i> stage	<i>Rubus</i> stage
<i>Acer pseudoplatanus</i>	r.—d.	—	—
<i>Betula alba</i>	r.—d.	—	—
<i>Cornus sanguinea</i>	o.—f.	r.—o.	r.
<i>Corylus avellana</i>	r.—l.f.	r.—o.	l.f.
<i>Crataegus monogyna</i>	o.	—	—
<i>Euonymus europaeus</i>	r.—o.	—	—
<i>Fagus sylvatica</i>	o.—d.	r.—f.	o.—l.f.
<i>Fraxinus excelsior</i>	o.—d.	o.—a.	o.—f.
<i>Hypericum androsaemum</i>	—	—	v.r.
<i>Ilex aquifolium</i>	r.—o.	r.	o.
<i>Ligustrum vulgare</i>	—	l.f.	—
<i>Lonicera periclymenum</i>	o.—l.a.	r.	r.—f.
<i>Quercus robur</i>	r.—o.	r.	—
<i>Rosa arvensis</i>	o.—l.a.	—	r.—l.f.
<i>Rubus caesius</i>	r.	—	—
<i>R. fruticosus</i> (agg.)	f.—a.	o.—d.	o.—d.
<i>Ruscus aculeatus</i>	v.r.	—	—
<i>Salix caprea</i>	o.—d.	—	—
<i>Sambucus nigra</i>	r.—l.a.	—	r.
<i>Sorbus aria</i>	r.	—	—
<i>Tamus communis</i>	r.	r.	—

<sup>1</sup> Compare the diagram on p. 44 which summarises the changes taking place in the subsidiary vegetation in the four different seres in the course of the life-history of the wood. These are described in detail in Section III.

# 34      *Development and Structure of Beech Communities*

*Flora of Gaps formed in the Beech Associes (sere 2) and during the Oxalis and Rubus stages of Consociation (sere 2) (continued).*

Woody Plants	Beech Associates (sere 2)	Consociation (sere 2)	
		Oxalis stage	Rubus stage
<i>Taxus baccata</i>	o.	—	—
<i>Viburnum opulus</i>	—	—	r.—l.f.
<i>Herbs.</i>			
<i>Agrostis tenuis</i>	r.—o.	—	—
<i>Ajuga reptans</i>	l.a.	l.a.	o.
<i>Arctium minus</i>	o.	—	—
<i>Arum maculatum</i>	—	—	o.—l.f.
<i>Asperula odorata</i>	—	o.	f.—a.
<i>Athyrium filix-foemina</i>	—	—	o.—l.f.
<i>Brachypodium sylvaticum</i>	o.—l.a.	o.	o.
<i>Bromus asper</i>	—	—	r.—o.
<i>Carex sylvatica</i>	r.—o.	o.	r.—o.
<i>Circaea lutetiana</i>	f.	f.—a.	o.—l.f.
<i>Dactylis glomerata</i>	r.	—	—
<i>Deschampsia caespitosa</i>	l.f.	o.	o.—f.
<i>Dryopteris filix-mas</i>	o.—l.f.	o.—l.d.	o.
<i>Epilobium angustifolium</i>	o.—f.	—	—
<i>E. montanum</i>	o.	o.—l.f.	r.—o.
<i>Euphorbia amygdaloides</i>	o.	o.	o.
<i>Festuca gigantea</i>	—	r.	—
<i>Fragaria vesca</i>	f.—l.a.	r.	—
<i>Galium aparine</i>	o.	—	—
<i>Geranium robertianum</i>	o.—l.f.	o.—f.	o.—f.
<i>Geum urbanum</i>	o.	—	—
<i>Hedera helix</i>	o.—a.	o.	o.—f.
<i>Hypericum hirsutum</i>	r.—o.	—	—
<i>Luzula pilosa</i>	—	r.	r.—o.
<i>Melica uniflora</i>	r.	r.—o.	o.
<i>Mercurialis perennis</i>	o.—d.	—	—
<i>Milium effusum</i>	—	l.f.—l.a.	o.
<i>Monotropa hypopitys</i>	—	—	r.
<i>Nepeta hederacea</i>	l.f.	—	—
<i>Oxalis acetosella</i>	f.—a.	f.—d.	a.
<i>Primula vulgaris</i>	r.—o.	r.	—
<i>Pteridium aquilinum</i>	o.—l.d.	r.—l.d.	o.l.
<i>Ranunculus auricomus</i>	—	r.	—
<i>Sanicula europaea</i>	—	r.	—
<i>Urtica dioica</i>	r.—o.	—	—
<i>Veronica chamaedrys</i>	o.—l.a.	r.	r.
<i>V. montana</i>	—	—	r.
<i>V. officinalis</i>	r.—o.	—	—
<i>Vicia sepium</i>	—	—	o.
<i>Viola sylvatica</i> (agg.)	o.—a.	o.—a.	f.—a.
<i>Mosses.</i>			
<i>Brachythecium purum</i>	r.	—	—
<i>B. rutabulum</i>	o.	l.a.	—
<i>Catharina undulata</i>	o.—l.a.	o.	r.—o.
<i>Eurhynchium piliferum</i>	—	r.	—
<i>E. praelongum</i>	o.—l.a.	o.—f.	o.—l.a.
<i>E. striatum</i>	o.—l.a.	o.—f.	f.
<i>Fissidens taxifolius</i>	r.—o.	o.—l.f.	o.
<i>Hylacomium loreum</i>	o.—l.f.	o.—l.f.	—
<i>H. triquetrum</i>	r.—l.a.	o.—l.f.	o.—a.
<i>Hypnum cupressiforme</i>	r.—o.	l.f.	o.
<i>Isoetecium myurum</i>	o.	—	—
<i>Mnium hornum</i>	r.—l.a.	—	—
<i>M. undulatum</i>	r.—l.f.	r.	r.
<i>Polytrichum formosum</i>	r.—o.	—	—
<i>Porotrichum alopecurum</i>	l.f.	—	—
<i>Thuidium tamariscinum</i>	o.—l.d.	o.—f.	o.—l.a.

As between different gaps formed in the associates or in one and the same stage of the consociation, there is considerable variation both in the frequency and degree of luxuriance of certain species. The following lists will convey some idea of the variations met with in gaps formed during the *Oxalis* stage.

Average diameter of gap	3 ft.	6 ft.	14 ft.	15 ft.	17.5 ft.
<i>Fraxinus excelsior</i>	—	o. (1 ft.)	o. (3 ft.)	o.—f. (1 ft. 9 ins.)	o. (10–12 ft.)
<i>Cornus sanguinea</i>	—	—	—	—	r
<i>Rubus fruticosus</i> (agg.)	o. (6–9 ins.)	o. (1 ft.)	l.d. (3 ft.)	f. (2 ft.)	l.f. (1–1½ ft.)
<i>Ajuga reptans</i>	—	—	l.	—	—
<i>Circaea lutetiana</i>	—	o.	l.f.	—	l.d.
<i>Dryopteris filix-mas</i>	—	—	—	—	o.
<i>Epilobium montanum</i>	—	—	o.	—	o.
<i>Euphorbia amygdaloides</i>	—	—	—	—	r.
<i>Fragaria vesca</i>	—	—	f.	—	—
<i>Geranium robertianum</i>	—	f.	f.	—	o.
<i>Hedera helix</i>	—	—	—	l.f.	—
<i>Milium effusum</i>	—	—	l.f.	—	l.f.
<i>Oxalis acetosella</i>	d.	d.	f.	f.	f.
<i>Pteridium aquilinum</i>	—	—	—	—	o.

The above diversity may be referred to several causes which will be dealt with seriatim.

1. The number and kind of species initially present will depend upon the stage reached by the wood when the gap is formed. Thus in the consociation the number of species initially present will be greater if the gap is formed during the *Rubus* stage than if formed during the preceding stage. Or if, by reason of the dominance of *Rubus* or *Ilex*, other species are excluded, then the degree of luxuriance of such plants will be greater. In other words, the flora of the gap when first formed partakes of the character of the general flora of the stage reached in the development of the associates or in the life-history of the consociation.

2. The supply of light admitted will depend partly on the height of the adjoining trees, partly on the density of the prevailing canopy and partly on the size of the gap. Upon this factor, assuming no other to be limiting, will depend not only the presence or absence of certain species but also the degree of luxuriance they attain, or in the case of woody perennials their rate of growth.

In the case of the *Oxalis* and *Rubus* stages of the consociation we are dealing with a canopy of uniform density (within the stage) and with trees of similar height. Hence variation in the gap flora will depend *inter alia* upon the size of the gap. The first three columns in the above list, obtained from gaps in the *Oxalis* stage, illustrate this point, increase in size of the gap giving a larger number of species. The same will also apply to the *Rubus* stage. A limit to this proportional variation will be set when the gap is large enough to allow the entrance of direct sunlight for a sufficiently long time to permit of the establishment of heliophilous plants.

The above will also apply to gaps formed in the beech associates, but the other factors governing light supply vary considerably. In the first place we



find a marked variation in the density of the canopy according to the proportions of the dominant trees—ash, oak and beech—present, and secondly the crown density of beech varies according to the competition experienced during growth. In the early stages of development of the associates, the pioneer beeches cast a heavy shade, whilst in the later stages the trees approximate in form and crown density to those grown in the consociation, and permit the growth of a varied ground flora. Thus the initial flora of a gap will vary according to the stage in development reached by the associates.

3. The above, however, does not offer a full explanation of the variation in the floras listed, for the number of species does not bear a fixed relation to the size of the gap. Species migrate with varying degrees of facility and an increase in the length of time during which the ground has been exposed will have an important bearing on the constitution of the gap floras. Thus the recently formed gaps will have fewer species present than those formed some years earlier. Again, in the beech associates, where the flora is more diverse, colonisation of the exposed area will be more rapid owing to the proximity of a greater variety of species and the same factor operates in retarding colonisation of a gap formed in the centre of a wood in the *Oxalis* stage. Thus colonisation by woody plants such as ash will be facilitated in the associates gap as compared with the *Oxalis* gap of the consociation owing to the presence of a relatively larger number of ash trees within the associates, for, as we shall see in Section III, the ash is almost eliminated from the consociation (sere 2) by the time the *Oxalis* stage is reached. A similar reason may be given in explanation of the absence of birch and the relative infrequency of oak. Further, initial dominance within the gap may be attained by a species because of its early arrival, and thus, compared with the mobile species, heavy-seeded species are placed at an initial disadvantage. The list of species compiled from the associates gaps bears this out, for very frequently the central portion of the gap is occupied by a dense growth of ash, birch, and occasionally sycamore, also *Salix caprea* and *Sambucus nigra*, forming an opener canopy. Oak, hazel, hawthorn and dogwood also occur, but only as comparatively infrequent constituents and not to the exclusion of other species. In the case of the ash there is this further initial advantage, that seedlings and young plants are almost invariably present and would take immediate advantage of the newly provided favouring conditions. Gaps are thus readily colonised by species with mobile fruits. In addition to this factor of mobility attention must be drawn to other factors of equal if not greater importance, viz., the age at which the various trees first produce fertile seed and the frequency of seed production. Regarding these, data obtained from various sources are presented for the principal trees here met with.

Reference to these data shows that not only is the heavy-seeded tree handicapped by reason of the weight of the seed but also by the delay in initiating reproduction and the periodic occurrence of the latter. For whereas

the average annual seed production is in the neighbourhood of 16.5 per cent. for oak and beech, that for birch and ash is 44.8 per cent. and 33.3 per cent. respectively, whilst the sycamore also produces seed annually after the 40th year. Thus the initial advantages are all with the light-seeded, and early and frequently reproducing species.

Species of tree	Age at which seed production begins		Average annual seed production in per cent. of full crop
	In open	In forest	
<i>Betula</i> sp.	10	20	44.8
<i>Fraxinus excelsior</i>	25	40	33.3
<i>Acer pseudoplatanus</i>	25	40	—
<i>Quercus robur</i>	60	80	17.1
<i>Fagus sylvatica</i>	40-50	60-80	16.2

The previous description applies to the consociation of sere 2. In sere 1, where *Rubus* appears before the seed-bearing age and would attain luxuriant development with the further opening up of the canopy with increasing age of the wood, the seedling must encounter considerable difficulty in its establishment. In sere 0, on the Chilterns, gaps are quickly overgrown by a dense tangle of *Rubus* which prevents successful beech regeneration. In these gaps, however, oak is a frequent constituent and under natural conditions probably prepares the way for beech establishment and growth. In sere 3 no difficulties of this nature are met with during the *Rubus* stage.

Attention may now be directed to the relation between the flora of the gaps and beech regeneration, in the light of the previously described phenomena.

1. That admission of light by a break in the canopy is necessary for successful regeneration has been demonstrated, so that any competition encountered by the beech and operating through the light factor will have a hostile influence upon beech establishment. If the gap is formed during the *Oxalis* stage, then, no opposition is immediately offered to the growth of the seedling by any of the species present, but the additional light admitted through the canopy during the *Rubus* stage may be cut off by the presence of the shrub layer. Jolyet says that the greatest obstacle to beech regeneration is the luxuriant growth of *Rubus* and Mr Hobart-Hampden has shown me an example of beech regeneration on the Chilterns rendered successful only by the systematic cutting over of the brambles. Clearly then it is advisable to initiate reproduction before the brambles can interfere with the growth of the seedling. Nisbet<sup>1</sup>, while pointing out that the age at which trees reach their greatest market value varies according to environmental conditions, gives a rough estimate of this age for a number of trees. For beech on good soil he puts the age at 90-120, and on inferior soil at 80-100. Exploitation of beech when it has attained its greatest market value therefore coincides roughly with the transition stage *Oxalis-Rubus* and this permits of the initiation of regeneration during the *Oxalis* stage (consociation—sere 2).

<sup>1</sup> *The Forester*, 1, 1905, p. 333.

2. Directing attention next to the relation of the size of the gap to beech regeneration, we first note that the minimum diameter will be the diameter of the crown of the tree removed. This will vary somewhat according to the position of the crown with relation to its neighbours and trees in process of elimination will have smaller crowns than those enjoying full sunlight.

It has been pointed out already that mast, when produced under forest conditions, is projected only a short distance from the perpendicular, while the majority of the nuts fall vertically downwards. Thus the proportion of the exposed area that will be colonised will depend on the size of the gap and the free play of wind. If the gap is small then the whole area may be seeded, and although unevenly distributed a sufficient number of nuts may fall in the centre to colonise the gap adequately, since during a good mast year there is a superabundance of seed. The larger the gap the smaller will be the proportion colonised, the seedlings being almost limited to the periphery of the gap. But in a large gap, and especially if there is a general thinning of the canopy, the wind will have freer play and seeds will be transported further, thus tending to diminish somewhat the proportion of the unseeded area.

The necessity for limiting the area exposed appears also in another connection. In a given sere the luxuriance of the subsidiary flora depends upon the number of trees per unit area. Thus in order to give the beech the greatest opportunity of establishing itself in the area seeded it is necessary so to regulate this number that luxuriant growth of competing species will not take place whilst yet admitting sufficient light for the growth of young beech. This applies particularly to the *Rubus* stage where, if the break in the canopy is large enough, brambles soon vegetate so luxuriantly as to exclude all other species of flowering plants by reason of the shade cast (in one example the light intensity under *Rubus* was 1/110). This however applies mainly to those seedlings which have sprung from seeds projected further into the gap than the vast majority, for where the peripheral zone of young beech occurs *Rubus* is generally so handicapped by the shade of the neighbouring canopy that it has no serious adverse influence on seedling growth. Clearly then the size of the gap must be regulated to admit sufficient light to the seedling and yet prevent luxuriant development of its competitors.

3. From a consideration of the foregoing paragraph the importance of the time factor will be realised. The longer the gap is exposed the greater is the likelihood of its colonisation by species absent from the immediately adjacent flora and their attainment of a greater height growth, and the smaller become the chances of the beech in competition with these. For the survival of the seedling, therefore, and more especially of those sprung from seeds thrown further into the gap than the rest, the time factor is of primary importance: that is to say, the seedling must have an opportunity of germinating and establishing itself before the area is occupied by such tall growing species as

*Pteridium aquilinum*, *Epilobium angustifolium*, *Rubus*, *Urtica dioica*, or the woody plants, ash, birch and sycamore. Thus to secure successful regeneration the formation of a gap must also coincide with a full mast year. Occasionally one meets with a gap completely colonised, and investigation reveals a decayed tree stump in the centre. The explanation seems to be that the tree was removed just after the heavy crop of mast had been shed, when the whole area underneath its canopy was abundantly seeded and the subsequent growth of the seedlings was unhindered by competition. On the other hand, in the beech associates there occur gaps from which young beech is entirely absent and this cannot be attributed to competition from taller growing plants. In such cases we may suppose that adequate seeding and seedling establishment have not taken place and that the gap has been formed subsequent to the last full mast year.

#### SUBSEQUENT DEVELOPMENT.

The best examples of beech regeneration have been observed in the beech associates of sere 2 and the following remarks apply in the main to regeneration as seen in this community.

The most characteristic feature of beech rejuvenation is the occurrence of a central core of varying constitution surrounded by a zone of beech, more or less pure. The most luxuriant growth is shown by the individual beeches occupying the centre of the gap, the height attained decreasing as the periphery of the gap is approached. This is correlated with the diminishing light supply, which as the branches close in upon the gap, falls to sub-optimal for the growth of young beech, which may become table-topped and finally die. Whether this will happen to all the young beeches in the gap will depend on the size of the gap, which will be closed in completely only when it is initially small. An example of this arrest in the growth of rejuvenating beech was seen in the *Rubus* stage of the consociation, where the closing in of the canopy had arrested the growth of the young beech when it had reached a height of about 30 feet. Sometimes a solitary individual survives, pushing its way towards the thinnest portion of the canopy. In the larger gaps there is a similar "slowing up" of the rate of growth of the marginal members, whose very small leaves and flattened crowns indicate mere existence conditions. No doubt too the unhindered growth of those individuals nearer the centre and the lateral extension of the parent crowns combine to exclude the light from the outer members of the circle.

The centre of a circle of rejuvenating beech is sometimes occupied by plants whose degree of luxuriance would not seriously handicap beech seedlings, and in this central area there is found with varying frequency a number of beech plants whose ages are decidedly less than those of the circle. The explanation seems to be that the admission of light to the parent crowns has promoted flower production and the ripening of seed, which, dropping from the laterally extended crowns, falls into the central area. The young plants thus observed

would be the offspring of a partial crop. This gradual closing of the gap will also tend to suppress the subsidiary flora and the seedlings' competitors.

Woody plants other than beech are more strongly represented in the beech associates than in the consociation. For this reason gaps in the latter are less often and to a less extent colonised by such plants as the ash. In the associates, however, gaps are readily colonised by the mobile species, ash, sycamore, birch, goat willow and the less frequent elder. These may or may not be associated with a peripheral zone of beech. In the latter case the formation of a gap has evidently not coincided with, or approximated in time to, a mast year, so that the whole exposed area is colonised by dense thickets of these mobile species, the most important of which is the ash. The appearance of these prevents the establishment of seedlings owing to the shade cast, as is indicated both by the ground flora and by light readings, which are subminimal for beech. This implies that no beech colonisation can take place until by subsequent growth and the reduction in the number of individuals the canopy opens out sufficiently to permit of beech invasion. The period at which this occurs will depend upon the species and is related to the light requirements of these. Thus sycamore will prevent beech establishment for a longer period than will ash or goat willow. In such "secondary consociates" the ground is generally almost devoid of leaf litter, and the predominating species of the ground flora are mosses, but *Rubus* frequently persists as a small plant about 6 ins. high. (For the flora of the "secondary consociates" of ash *v.* Section I, 12, pp. 172 to 175). With an increase in the age of the dominants the canopy opens out and other shade-tolerant species commonly met with in the beech associates appear. About this time beech is able to colonise and young beech trees from 5-28 ft. were observed under a canopy of ash 50-65 ft. in height. In this way the presence of these trees may hold up beech regeneration for a period, but their ultimate effect is to facilitate the progress of the beech, towards dominance, since on certain soils colonisation by *Rubus* and *Pteridium* may more effectively prevent beech establishment and thus delay the normal succession.

When the colonisation of a gap dates from a full mast year, we may expect beech and most frequently ash to occur mixed and in varying proportions within the gap. In the centre ash is dominant with an occasional to rare beech; in the peripheral zone beech is dominant with occasional to frequent ash (Fig. 2). The light-demanding ash is here handicapped by the shade cast by the adult beech, and although it survives as a straggling sapling for 12-15 years it ultimately yields to the beech. In the centre however the access of light allows the ash to make headway whilst the associated beech die or persist as spindly saplings. In Fig. 3 is depicted a later stage of development. Here the parent trees have been removed but the reproduction circle, with peripherally dominant beech and centrally dominant ash, can be made out. Here the ashes are surpassed by the peripheral beech and ultimately yield before beech pressure except one or two which may survive and reach

the full height of the canopy. The spindly beech saplings in the centre may recuperate when the ash opens out but have little chance of survival when the crowns of the marginal beech converge on the centre.

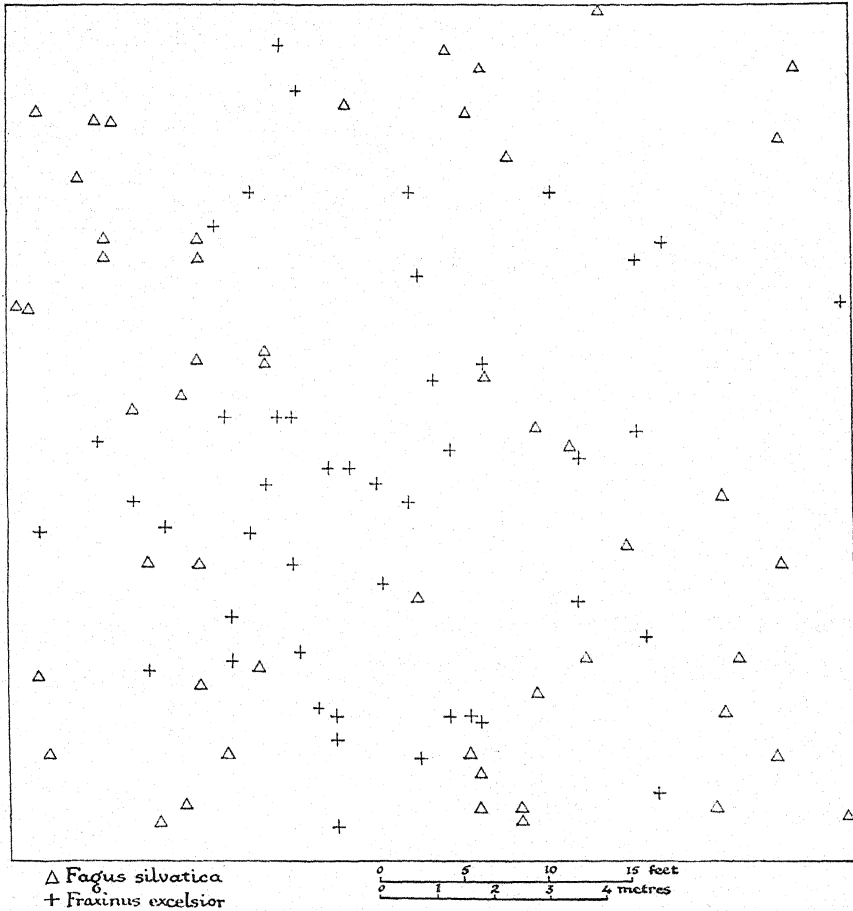


FIG. 3. Reproduction Circle in beech consociation (sere 3) showing later development. Age about 45 years (1922). Young beech is dominant round periphery, ash with a little beech in the centre.

Under primeval conditions when seedlings of partial crops survive, the natural beechwood would be of an uneven aged character, with a large proportion of trees of like size, dating from the periodic full mast years. But where the crop is practically limited to these years, as under present day conditions, there is a marked tendency for the wood to assume an even-aged character. This is well exemplified by the consociation nuclei and the later stages of the beech associates development. These sometimes occupy considerable areas and approximate to the consociation in general characters. When the

whole woodland is even-aged the effect is due to the removal of the parents and the direct encouragement of young growth.

The dense thickets of beech, ash, etc., which occupy the gaps kill out the subsidiary vegetation, with the result that in consociation nuclei and in the consociation itself the subsidiary flora arises *de novo*, and although related to, is not directly descended from, the flora of the beech associates.

### SECTION III.

#### THE BEECH CONSOCIATION.

##### GENERAL DESCRIPTION.

The beech consociation occupies a considerable area of the district investigated, and is represented by East Dean Wood, Charlton and Singleton Forests. Similar woods occur on the West Dean estate a few miles to the west, but these are known to be planted.

The climax consists of an almost pure beechwood, whose constituent members have grown up in competition with each other and with other tree species of similar growth form. Thus we have an entire absence of pioneer forms, whose shorter boles and larger and more spreading crowns developed under opener conditions are features of the associates. A striking feature of the beech consociation is its remarkably uniform and even-aged character, for which the restriction of successful regeneration to full mast years must be held in part accountable. In the production of this result, it is extremely probable, and in the case of Singleton Forest authenticated, that the parent trees have been removed.

The prevailing idea of the structure of a beechwood is that it consists of a canopy of dominating beech with a ground flora of a few isolated plants mostly showing obvious relations to the prevailing gloom during the shade phase or of species which take advantage of the short available period of the light phase<sup>1</sup>. But the growth forms represented, at least in the British semi-natural beechwoods, are of a more varied character than is brought out by the existing descriptions, and show variation both in the number and abundance of species, which is correlated with the structural development of the wood and with the sere to which it belongs.

The method of treatment of the morphology here adopted differs from those hitherto used<sup>2</sup>, and consists essentially in describing changes in the vegetation accompanying increase in height and age of the dominant trees. In the initial stage of the consociation's life-history the trees occupy the ground to the exclusion of all but a few isolated and dwarfed ground species; and the period during which such conditions prevail will be referred to as the "Bare Stage." With advance in age of the wood there is an appreciable

<sup>1</sup> Warming-Graebner, *Lehrbuch der ökologischen Pflanzengeographie*, 1914-18, p. 560.

<sup>2</sup> Rübél, *Geobotanische Untersuchungsmethoden*, 1922, p. 179, *et seq.*

diminution in the density of the stand and the canopy opens out, admitting a light supply adequate to the needs of shade-bearing species. The further reduction in the number of trees per unit area is reflected in the greater luxuriance of certain species and in the first appearance of others. Two stages in this process are to be distinguished and are designated by the plants respectively most characteristic of them, viz., *Oxalis acetosella* and *Rubus fruticosus* (agg). In future these three stages will be referred to as the "Bare," "*Oxalis*" and "*Rubus*" stages, and just as we speak of a seasonal rhythm in the ground flora so we may refer to the changes during the lifetime of a wood (from the seedling stage to maturity) as the life cycle rhythm. It goes without saying that these divisions are not absolute, that there are transitional stages: these however are quite easily recognisable by their sharing some of the characters of the adjoining main stages. For these last it may be claimed that their relation to the structural development of the woodland is so close and easy of recognition as to warrant their choice in a description of its morphology.

In the woodlands investigated there is a remarkable uniformity in the constitution of the tree-layer—beech everywhere forming more than 90 per cent. of the wood—and this similarity extends *on the whole* to the species of the subsidiary vegetation. Differences in the latter occur and these will be referred to later, but the most marked variation relates to the *time of appearance* of certain species during the life history of a woodland. In some the *Oxalis* and *Rubus* stages appear before the woodland has attained the age of 70 years, whilst in others the appearance of *Oxalis* is delayed until after *Rubus* has become abundant, with *Ilex aquifolium* locally dominant, in a wood over 120 years of age. This variation in the time of appearance and period of dominance of *Oxalis* in the life cycle has been used as a basis in the classification of South Downs plateau beechwoods (seres 1, 2 and 3).

The beechwoods on Chalk described by Adamson<sup>1</sup> are distinguished by the absence of *Oxalis* (sere 4), whilst the regular exploitation of the Chiltern plateau beechwoods (sere 0) prevents the satisfactory application of this idea, although gaps in a 70-year old planted wood of slow growth occasionally show a central core of *Rubus* with a periphery of *Oxalis* indicating a difference in the time of appearance during the life history of a normal wood.

Apart from sere 0 where the evidence obtainable was not considered sufficient to indicate exactly the limits of the life cycle changes, the classification of the South Downs beechwoods may be presented diagrammatically (Fig. 4, p. 44).

An analysis of Fig. 4 shows that *Oxalis* dominates in sere 1 woods for a period of about 10 years when the wood is from 55 to 65 years of age. Thereafter *Rubus* assumes dominance. In sere 2 there is a delay in the first appearance of *Oxalis* until the wood has reached the age of about 80, after which for a period of at least 20 years this plant remains dominant. The dominant rôle is then assumed by *Rubus*. In sere 3 *Rubus* appears first with *Ilex aquifolium*.

<sup>1</sup> "The Woodlands of Ditcham Park." This JOURNAL, 9, see pp. 122-124.



*folium* locally dominant in a wood of upwards of 120 years of age. Thereafter *Oxalis* comes in. Finally in sere 4 *Oxalis* is not recorded and *Rubus* does not contribute much to the subsidiary flora.

In each wood examined sample plots of 100×100 ft. (or in the case of the younger woods 50×50 ft.) were measured. Data were obtained regarding the total number of stems, the height attained, the girth at 4ft. 3 ins. (breast height) from the ground, and the approximate age. The age of the younger woods (up to 70 years) was obtained by felling an ash tree and making a ring count, but the age of older woods was estimated, and is very approximate except in the case of the mature woods of seres 2 and 3 where cut stems were available. At the same time a classification was made of the crown strata into the four groups "dominant," "subdominant<sup>1</sup>," suppressed and dead. All the above data are collected and presented in Table I (v. p. 46).

Sere 4	No Oxalis														
" 3	Bare												Rubus Oxalis		
" 2	Bare								Oxalis			Rubus			
" 1	Bare					Oxalis		Rubus							
YEARS	0	10	20	30	40	50	60	70	80	90	100	110	120	130	140

FIG. 4. Diagram illustrating periods at which *Oxalis* and *Rubus* become dominant in beechwoods belonging to seres 1-4.

In Section II it was shown that the regenerating beechwood consists of a mixture of ash and beech. With increase in age there is a gradual reduction in the total number of stems until finally in the mature wood there remain about 23 to 10,000 sq. ft. Of these the vast majority are beech whilst an occasional ash and oak persist. Thus even although the ash start numerically equal to beech the majority are eliminated, as may be gathered from the data of the number of stems per unit area recorded from various stages in the life history of beechwoods (v. Table I, p. 46).

With an adequate light supply ash first grows more rapidly than beech and in this way maintains itself for a number of years in intimate mixture with the latter. Later the rate of growth of the beech is faster than that of ash with the result that the ash is surpassed, relegated to a subordinate position and finally practically eliminated. It is of interest therefore to inquire at what stage in the life history of the wood beech definitely assumes leadership, and how beech and ash behave in the various seres.

In Section I, Table V, 12, p. 197, the required data are summarised but may

<sup>1</sup> These terms are here used in the sense of the silviculturist and when so employed are written in inverted commas. A tree in canopy is "dominant" when one half or more of the crown is fully exposed to the light, "subdominant," when less than one half is fully lighted—the crown as a whole being lower than the crowns of "dominants." A suppressed tree is one wholly shaded.

be repeated here for convenience. In a young wood of mixed ash and beech belonging to sere 4, the beech surpasses the ash at a height of 35 ft. In sere 3 the ash at 45 years of age has attained a height of 52 ft. and is definitely surpassed by the beech. In sere 2 the ash at 66 years of age is relegated to the "subdominant" layer<sup>1</sup> and appears from 5-10 ft. shorter than the "dominant" beech whilst in sere 1 several ash, aged 67, and about 70 ft. in height are still holding their own with beech but are now not quite so tall. Thus as we pass from seres 4 to 1 conditions favour the ash relatively to the beech but there is no evidence to show that the growth of beech is adversely affected. The result is that a wood of almost pure beech is developed most quickly in sere 4 and progressively less so in seres 3, 2 and 1.

The lack of definite information as to the age of the woods except in the case of the younger ones prevents a close comparison of the density of stand and the relation of beech to ash in the various stages of the several seres. Woods 3 (*Rubus* stage, sere 1) and 4 (bare stage, sere 2) are however of equal age and may be compared. The total number of stems per unit area in sere 1 is 132, and in the sere 2, 108. The analysis of the data shows a denser stocking of "dominant" beech in sere 1 (48) than in sere 2 (32). Similarly with ash (and oak). The examination of the crown strata other than "the uppermost" shows that the sere 2 wood is in a more advanced stage of development than the wood of equal age belonging to sere 1; for whilst the majority (in the sample analysed, all) of the standing beech trees in the latter are still living, a large proportion in the former are dead. A similar deduction may be drawn from an analysis of the data respecting the ash. These data seem to warrant the conclusion that competition is keener in sere 2 than in sere 1. Further the rapid elimination of ash in sere 3 and the reduction in the number of crown strata to one indicate that competition is more severe in sere 3 than in sere 2. From the fact that beech surpasses ash at 35 ft. in sere 4, the above may be extended to include this sere where it may be fairly concluded that competition is the most severe of all. No data are available respecting sere 0. Data regarding the ultimate height growth are available only from seres 2 and 3, where the average height attained is 100 and 90 ft. respectively.

#### SOIL.

The general character of the soil has already been described<sup>2</sup>. The average depth of the loam with the extremes in brackets are given in Table I and bear out the previous description. Sere I woods grow on a compact loam. Sere 2 woods occur on a soil with or without loam—in the former case opener in texture and on the whole shallower than in sere 1. In sere 3 the calcareous soils are of more general occurrence but a shallow loam occupies part of the area. The total depth of exploitable soil increases from sere 3 to sere 1.

<sup>1</sup> Wood 5 shows affinities with sere 1, and is not regarded as typical of sere 2.

<sup>2</sup> Introduction to Part II. This JOURNAL, 12, 1924, p. 150.

## Development and Structure of Beech Communities

TABLE I.

Reference No. of Wood ...	Sere 1			Sere 2			Sere 3		
	Bare	<i>Oralis</i>	<i>Rubus</i>	Bare	Pre- <i>Oralis</i>	Pre- <i>Oralis</i>	Bare	Late Bare	Late Bare
1	176	168	96	80	108	60	208	44	37
2	44	32	36	24	16	0	176	—	—
3	—	—	—	4	—	—	—	—	—
4	64	80	48	32	48	48	—	—	—
5	24	8	8	0	12	0	—	—	—
6	—	—	—	4	—	—	—	—	—
7	60	24	20	8	36	12	—	—	—
8	16	20	24	20	4	0	—	—	—
9	—	—	—	—	—	—	—	—	—
10	48	56	28	16	20	—	—	—	—
11	0	0	0	0	0	0	—	—	—
12	4	8	0	24	4	0	—	—	—
13	4	4	4	4	0	0	—	—	—
14	63	64	70 +	70	80?	100?	52 +	95	90-100
Total No. of stems: <i>Fagus</i>	2' 1 1/2"	2' 2 1/2"	2' 8 1/2"	2' 7"	2' 6"	3' 2 3/4"	100	100	100
" " <i>Fraginus</i>	50	55	67	66	80?	90?	—	3' 3"	3' 9"
" " <i>Quercus</i>	1/37	1/41	1/38	1/31	—	—	45	90?	100?
No. of "dominant" <i>Fagus</i>	6-1	6-1	6-1	6-1	—	—	1/42	1/21	1/22
" " <i>Fraginus</i>	26	25	20	18	14	20	7-2	—	6-4
" " <i>Quercus</i>	6-1	6-1	6-1	6-1	6-3	7-1	12	9	8
No. of "subdominant" <i>Fagus</i>	(20-29)	(20-28)	(16-30)	(9-24)	(10-21)	(16-27)	(0-12)	(0-15)	(0-11)
" " <i>Fraginus</i>	(23-29)	(23-29)	(16-30)	(9-24)	(10-21)	(16-27)	(0-12)	(0-15)	(0-11)
" " <i>Quercus</i>	(23-29)	(23-29)	(16-30)	(9-24)	(10-21)	(16-27)	(0-12)	(0-15)	(0-11)
Suppressed <i>Fagus</i> ...	—	—	—	—	—	—	—	—	—
" <i>Fraginus</i> ...	—	—	—	—	—	—	—	—	—
Dead <i>Fagus</i> ...	—	—	—	—	—	—	—	—	—
" <i>Fraginus</i> ...	—	—	—	—	—	—	—	—	—
Height in feet of "dominant" <i>Fagus</i> ...	—	—	—	—	—	—	—	—	—
" " <i>Fraginus</i> ...	—	—	—	—	—	—	—	—	—
" " <i>Quercus</i> ...	—	—	—	—	—	—	—	—	—
Average girth of "dominant" <i>Fagus</i> ...	—	—	—	—	—	—	—	—	—
Approximate age	—	—	—	—	—	—	—	—	—
Light intensities	—	—	—	—	—	—	—	—	—
H-ion concentration (surface 1 1/2" of soil) ...	—	—	—	—	—	—	—	—	—
Av. depth of loam in ins. (with extremes in brackets)	(23-29)	(20-28)	(16-30)	(9-24)	(10-21)	(16-27)	(0-12)	(0-15)	(0-11)

## WATER CONTENT.

Samples of soil at 0-2 ins., 6-8 ins., and 18-20 ins. depth were collected from the three stages of seres 1, 2 and 3, for their water content determination. The data obtained showed no consistent relation to the different seres. The  $\frac{\text{water content}}{\text{humus}}$  ratio was also determined, but again no correlation was established. General field observations supported by observations on plant growth indicate that sere 1 soil is wetter than sere 2, and sere 2 than sere 3. In the sequel reliance is placed on these observations since single determinations of the moisture content cannot be relied upon to give a true idea of the relative wetness of the different soils.

## HYDROGEN-ION CONCENTRATION.

The data already given are supported by the data for the consociation. On the whole there is a gradual increase in acidity as we pass from sere 3 to 1, but here again it may be pointed out that there is no necessary correlation between floristic type and this factor.

## LIGHT INTENSITIES.

The data respecting density of stocking indicates that there is no direct relation between the occurrence of the Bare-soil-*Oxalis-Rubus* succession and light intensity. The light values<sup>1</sup> obtained during the summer of 1923 and summarised in Table I show that *Oxalis* is absent from the Late Bare stage in sere 3 with a light intensity of 1/21 whilst it is present in sere 1 under a light intensity of 1/41.

## THE ROOT SYSTEM OF THE BEECH.

According to Jolyet<sup>2</sup>, "At first the taproot (of the beech) remains simple and penetrates the soil as far as the shoot rises above it; at about 12 or 15 years of age the taproot ceases growth and lateral roots extend; at 30 these cease to elongate and are then replaced by superficial spreading roots often projecting above the soil to some distance from the base of the tree." On the Chalk the root system varies in depth according to the depth of the soil. Where the latter is shallow most of the finer roots occur in the upper few inches and with a maximum root penetration of about 24 to 30 ins. down to the solid chalk. Beech can however attain fair dimensions on shallower soils. On the Chilterns the root system of a beech had been exposed on one side as far as the stem by quarrying and the whole was confined to the surface 9 ins.—the under surface forming a perfectly flat horizontal projection, no roots penetrating the solid chalk. Where the soil is deeper, as for example where residual deposits have accumu-

<sup>1</sup> These values are expressed as fractions of bright sunlight in the open. They were obtained by a Watkins Bee-Meter moved in straight lines through the wood and thus exposed to sunflecks as well as to shade. They are not comparable with the data given in Part I. (This JOURNAL, 11, 1923, p. 43.)

<sup>2</sup> *Traité Pratique de Silviculture*, 1916, p. 217.

lated, beech roots penetrate to a depth of at least 4 ft. The root system then may be accurately described as accommodating, and part of the success of the beech in competition with oak and ash on the shallower soils of the Downs may be attributed to the possession of a type of root system in which the production of an extensive system of surface feeding laterals may effectively replace the deeper going root system which is formed on suitable soils of greater depth. Occasionally knee-like projections from the roots of older trees appear at varying distances from the butt and from these there frequently arise shoots from 4-6 ft. in height with a table-topped branch system. These often convey the false impression of natural regeneration from seed. On the whole, on the shallower soils throughout the beechwood area the beech shows this extensive development of comparatively slender superficial roots, proclaiming the tree as mainly a surface feeder. No information is available as to the character of the beech root system in the deeper soils of the Chilterns Plateau. In shallow soil and especially along the brow of escarpments where the surface litter is blown away, sometimes also on siliceous soils, as for example in some places in the New Forest, the larger radiating roots only half buried in the soil may be observed. In Burnham Beeches this feature had attracted the attention of the poet Gray who immortalised it in his *Elegy* in referring to a beech "that wreathes its old fantastic roots so high." The superficial character of the root system of the beech must have an important effect on the ground flora, for the surface feeding roots come into direct competition with, and exploit the same soil layers as, the herbaceous species.

The species occurring in the woods examined are listed on pp. 50, 51.

#### THE BEECH CONSOCIATION OF *SERE* I.

This consociation occupies a rather limited area in the western portion of Singleton Forest. The woods examined varied in age from 50-70 years and all three stages were observed, but this limitation in age prevents the description of a mature wood and an account of a more typical Bare-stage. The woods were examined during the summer of 1922 and the early spring and summer of 1923, but no comparison of their appearance with that for 1921 is available.

##### *Bare-stage*<sup>1</sup>.

The wood examined is in the late Bare-stage just prior to its passage to the *Oxalis* stage.

*Tree-layer.* The composition of the wood may be gathered from the data analysed in Table I, column 1. At an age of 50 and a height-growth of about 60 ft., the "dominant" trees are chiefly beech, but fully 50 per cent. of the

<sup>1</sup> Although described as "Bare," it may be pointed out that certain plants do occur, but their presence does not interfere with the general impression of a bare forest floor. Needless to say, the word is used in the sense of "no vegetation" and does not refer to the leaf litter which throughout the woods described is from 1-1½ ins. deep.

ash stems retain their position with beech. Attention may be drawn here to the fact observed in all the woods that only two classes of living ash exist, thus indicating the inability of the ash to withstand suppression at the pole stage. The oak is an occasional constituent.

*Subsidiary layer.* All the plants (except *Monotropa*) are undersized and scarce, but it is of interest to note that *Rubus* persists as a small plant of 2-3 ins. The persistence of *Rubus* under shade has been noted by Wilson<sup>1</sup>, who cites Dobner<sup>2</sup> as having made a similar and earlier observation. Seedling ash up to 6 years and showing very slow growth, are frequent. *Hedera* appears in small patches and *Viburnum opulus* is a small and rare plant. Of the herbaceous plants it may be noted that *Oxalis* is invading from the pathways and in 1923 has appeared as an occasional constituent through the wood. The mosses, partly because the leaf litter is rather thick upon the ground, are poorly represented in species and individuals.

*Oxalis stage.*

*Oxalis* appears generally throughout the wood when the latter is between 50 and 55 years of age and remains the dominant plant for about 10 years.

*Tree layer.* There is a reduction of 20 in the total number of stems (Table I, column 2). In 5 years 8 beech and 12 ash have been eliminated. There is also a reduction in the number of "dominant" ash, but as might be expected an increase in the "subdominant" class. The age of the wood is 55 and the height of a felled tree 64 ft. The oak remains an occasional constituent.

*Subsidiary layer.* In addition to the woody plants occurring in the Bare stage the following have made their appearance: *Euonymus*, *Ilex*, *Ligustrum*, *Ruscus* and *Taxus*, as rare to occasional members. There is a considerable increase in the number of herbaceous plants, among which in the order of descending frequency, *Oxalis*, *Viola sylvatica* (agg.) and *Melica uniflora* are the most important. There is also an increase in the number of mosses both in species and individuals but on the tree stems bryophytes are limited to the bases.

*Rubus stage.*

In this sere the *Rubus* stage begins when the wood has reached about 65 years of age. The wood examined is only a year or two older than this, so that a typical *Rubus* stage is not presented, thus prohibiting a strict comparison with the mature woods of seres 2 and 3.

*Tree-layer.* The total number of stems is now reduced to 132 per unit area (Table I, column 3). The most interesting fact shown here is that in a wood 67 years of age and 70 ft. tall, 8 ash trees have retained "co-dominance" with beech, whose rate of growth as compared with that shown in sere 2 (v. Table I, column 4) is at least maintained. The oak also holds its own, with beech as an occasional constituent.

<sup>1</sup> Ann. Bot. 25, 1911, p. 46.

<sup>2</sup> Botanik für Forstmänner, 1882.



[illegible]



*Shrub layer.* The dominant shrub is clearly *Rubus*, which although it does not cover the ground so completely as in the mature wood of sere 2, nevertheless may attain a height of two feet, the average being about 18 inches, and shows quite a vigorous and robust appearance. *Ilex* is occasional to frequent but is a small plant, as are also *Euonymus*, *Viburnum opulus* and *V. lantana*, which range from 6–9 ins. in height.

*Ground flora.* The species present are almost the same as those recorded from the *Oxalis* stage, with the noteworthy addition of *Veronica chamaedrys*, but there is a general increase in their frequency, this being particularly the case with *Asperula odorata*, *Luzula pilosa*, *Melica uniflora*, and *Dryopteris filix-mas*. There is an apparent reduction in the frequency of *Oxalis*, which on the whole did not appear so vigorous in the woods belonging to sere 1 as in the older woods belonging to the *Oxalis* and *Rubus* stages of sere 2.

Mosses are much more apparent in the flora due in large measure to the increased frequency of *Hylocomium triquetrum* and *Thuidium tamariscinum*. Bryophytes occur on but are limited to the bases of the trees.

#### THE BEECH CONSOCIATION OF SERE 2.

Woods belonging to the climax stage of this sere cover a large part of our area, most of them being in the *Oxalis* stage of development. Although exact limits have not been set to the 3 stages it is believed that the Bare stage terminates when the trees attain an age of about 70 years. *Oxalis* dominates in woods from 80–100 years of age, but in some cases at least its appearance and dominance are delayed for several years. This transitional period is denoted as the pre-*Oxalis* stage. *Rubus*, which is occasional to frequent in the *Oxalis* stage, multiplies rapidly and dominates in woods from 120–140 years of age.

##### *Bare Stage.*

This was shown by one wood of rather limited extent.

*Tree layer.* Data regarding this layer are collected and analysed in Table I, column 4. The total number of stems per unit area is 104, showing a reduction of 28 as compared with the wood of similar age in sere 1. If we deduct the number of dead stems the difference is much greater. The floor of the wood was littered with the fallen stems of beech and ash but principally of the latter. The tallest ash here are definitely relegated to the “subdominant” class, and altogether the wood is in a more advanced stage of development than the wood of similar age referred to. The oak is an occasional constituent and maintains itself in competition with the beech.

*Subsidiary flora.* In this wood beech seedlings occur, but under the prevailing conditions, they survive only a month or two, death occurring in June and July. No young beech older than this has been found. Clearly then under the existing conditions beech regeneration cannot take place at this stage—even if the parents bore an adequate supply of fruit.

We have already seen that ash in the pole stage is intolerant of shade. This, however, is not the case with the seedling, which survives for at least 6 years under the deep shade of the Bare stage. It is true that the plants are small, with spindly stem, slow rate of growth and with an average of only two small trifoliate leaves, yet they manage to survive under conditions prohibitive to beech.

*Hedera* is strictly confined to the trees, there being no ground societies which are a feature of the later stages. During the summers of 1922 and 1923 no *Rubus* was observed in the area. No *Taxus* older than the seedling stage was found.

Herbs are poorly represented and all are undersized.

Mosses are well represented in species and occur chiefly on the decaying stems and on mole-hills. The living tree-trunks are without any bryophytic covering.

#### *Pre-Oxalis Stage.*

Two woods which, from the height of the trees and the general appearance of the subsidiary flora, were expected to show dominant *Oxalis*, showed the plant in patches only. It appears first along the brows of terraces, near forest tracks, sometimes at the bases of trees, in the neighbourhood of small gaps and where the loam is deeper. For example, a loam covering of 27 ins. depth carried *Oxalis*, whilst the plant was absent from a loam 18 ins. deep. *Oxalis* was observed occurring on terraces and deeper soil in the beech associates of sere 3 whilst it was generally absent from the rest of the wood<sup>1</sup>. It is probable that the factor common to all these habitats and permitting the appearance of *Oxalis* is an adequate water supply. The evidence available seems to indicate that in a few years time the changes accompanying a thinning of the canopy will permit of a continuous *Oxalis* carpet in which are set the scattered individuals that make up the remainder of the subsidiary vegetation.

*Tree-layer.* In columns 5 and 6 of Table I, data regarding the trees are analysed. Column 5 presents data showing similarity in density of stocking, and in dominant ash, to the *Rubus* stage of sere 1, whilst column 6 contains the data of a wood which is almost pure. It is interesting to observe however that the same number (48) of "dominant" beech is recorded from the pre-*Oxalis* woods and from the *Rubus* wood of sere 1. The oak is an occasional to rare constituent and in one wood *Castanea sativa* is occasional.

*The Subsidiary layers.* An incipient discontinuous shrub layer consisting of *Rubus* has made its appearance. The arching stems of neighbouring plants do not intertwine but may attain exceptionally a length of 2½ feet; the average is from 6–9 ins. Very straggly *Ilex* bushes with few leaves and up to 4–5 ft. are locally frequent. Their general appearance is similar to that shown by much of the *Ilex* in the calcareous parts of the *Rubus* stage of sere 3. *Hedera*

<sup>1</sup> Section I, 12, p. 191.

occurs in both woods, in one (wood 5) it is scattered and forms no pure societies, in the other it is frequent as a climber and is locally dominant on the ground. *Viburnum opulus* with a height of 12 ins. in the former wood and 2-3 ins. in the latter is an occasional constituent. Young ash plants again showing a slow rate of growth are frequent.

The herbaceous flora is essentially similar to that of the *Oxalis* stage except that in the latter the ground is carpeted with *Oxalis* and *Viola sylvatica*. Indeed the presence of this green background in the *Oxalis* stage tends to obscure the low-growing *Rubus*, which is thrown into relief against the brown leaf-litter in the pre-*Oxalis* stage. The other herbs are scattered and undersized.

The development of the subsidiary flora, which includes *Asperula*, *Deschampsia caespitosa* and *Melica uniflora*—plants which in this sere are recorded only from the *Rubus* stage—suggests affinities with sere 1 where they all occur in the *Oxalis* stage. This is also supported by the density of the trees and the persistence of ash. On the other hand, *Oxalis* is colonising suitable centres and presumably will become more general with a reduction in the number of trees. In one of the woods the surface 2-3 ins. of soil was extremely open, porous and dry—a condition of affairs which would handicap shallow rooting species but would not interfere with the growth of deep rooters once these became established. These two woods are provisionally assigned to sere 2.

#### *Oxalis* Stage.

Three woods showing this stage were examined. Despite differences in the chemical composition of the superficial soil layers and in the hydrogen-ion concentration the flora is remarkably uniform. Woods 7 and 8 occur on a west facing slope and show a luxuriant growth of *Oxalis*, whilst in the older wood 9—whose soil is in parts loamy and in parts calcareous—the plant is less robust.

*Tree-layer.* As compared with the bare stage the floor of the wood is remarkably free from dead stems, for by this time beech has asserted its supremacy, the majority of the ash has been eliminated and the stems decayed. Part of the result may be due, in the case of woods whose trees have reached exploitable dimensions, to the deliberate and periodic removal of trees other than the "dominants." This system, pursued for a number of years on the Goodwood estate, does not therefore appreciably interfere with the natural development of the beechwoods. This is borne out by the fact that the number of "dominants" in the *Oxalis* stage is similar to that in the late bare stage described, the difference in the total number of stems being due to the ash and the beech stems other than "dominant." In this sere observations seem to indicate that *Oxalis* appears just about the time when most of the ash are eliminated. Any ash trees maintaining themselves at this stage are likely to persist into the *Rubus* stage. The oak is an occasional constituent of the tree layer.

*Subsidiary layer.* Compared with the Bare stage there is an increase in the number of woody plants but all are of small size and indicate the operation of some limiting factor. These plants are practically the same as those making their first appearance in the *Oxalis* stage of sere 1.

In the *Oxalis* stage the beech seedling does not die so soon as in the Bare stage but survives a number of years. Young plants up to 5 years of age have been found but not older and decrease in the successive annual growths indicates the unsuitability of the environment for successful reproduction whilst the present conditions prevail. Data regarding the rate of growth are given in Part I<sup>1</sup>. In Germany it is the practice to initiate beech regeneration when *Oxalis* makes its appearance.

Here too young ash survives much longer, frequently attaining an age of 25-30 years with a stem a foot to a foot and a half long. The latter however lies prostrate on the ground, rooting at the nodes with only the terminal 6 ins. or so erect and generally bearing 2-4 leaves, evidently just sufficient to maintain life and a feeble growth. In some woods, however, these young ash trees are severely handicapped by being cut over periodically by rabbits and hares and 2-3 year old shoots resembling seedlings arise from comparatively stout rootstocks. In this way the young ash shows a considerably greater capacity to recover from cutting over than young beech.

An interesting record is that of a seedling of *Castanea sativa* in the heart of a beechwood and some hundred yards distant from the nearest possible parent. Mr Tansley informs me that he has seen good self-sown chestnut seedlings more than once on the Lower Greensand in Hants and West Surrey. Wilson<sup>2</sup> in reference to woods in North-East Kent says: "In this part of England mature specimens of the chestnut only produce ripe seed in unusually long and warm summers. . . . No seedlings have ever been found." This seedling (recorded in 1922) is therefore the result of the production of ripe fruit during the sunny summer of 1921 and its appearance indicates the possibility of some chestnut in our woodlands being subspontaneous<sup>3</sup>.

*Rubus* is an occasional constituent, its stems sometimes reaching a length of 3½ ft. but the average is about 6 ins. *Rosa arvensis* remains small. *Euonymus* and *Ligustrum* produce prostrate stems from which short shoots arise.

The facies of the herbaceous flora is due to the presence of *Oxalis*, whose dominance is sometimes shared by *Viola sylvatica* (agg.) and replaced by local societies of *Hedera helix*. There is a notable increase in the number of species in comparison with the Bare stage but nearly all are rare or occasional. *Mercurialis perennis* is confined to the better lighted margins of the woods and is not strictly speaking a member of the *Oxalis* flora.

Little change has occurred in the moss flora, although species frequency has slightly increased. It may here be noted that bryophytes were present

<sup>1</sup> This JOURNAL, 11, 1923, p. 43.

<sup>2</sup> L. c. p. 879.

<sup>3</sup> Cf. Summerhayes, Cole and Williams, this JOURNAL 12, p. 301.

on the trunks of the trees of wood 9 but absent from those of the other two.

The *Oxalis* stage reflects the beginnings of the lightening of the canopy and marks the initial endeavours of the wood at regeneration. A gap here and there is formed by the death of a tree but such gaps are generally partially closed by the lateral extension of the adjoining crowns sufficient to exclude an adequate light supply for the growth of young beech. If, however, the break in the canopy is of greater extent, then, if other conditions are suitable the beech has an opportunity of stocking the vacant ground.

It is interesting to examine a little more in detail the flora of these gaps formed by the fall of a tree or occasionally of two adjacent trees. These so far as my observations go occur chiefly in the later *Oxalis* phase, for the typical *Oxalis* stage is remarkably free from dead prostrate stems, indicating that the time of greatest competition has passed. And the death of a tree during this later phase generally implies a break in the canopy whilst the elimination of a "subdominant" or suppressed tree at an earlier stage does not.

The flora of these gaps already listed in Section 2, pp. 33 and 34, reflects the improved habitat conditions. Certain species appear for the first time in the life-cycle of the wood and give us an index of the species likely to appear in the later phase.

Not only do we have the appearance of new species but a greater degree of luxuriance of those already present. *Oxalis* forms a dense carpet in some but in others it is relegated to the shade of the beech canopy by reason of the denser shade cast by the leaf-mosaic of the taller *Circaea*. *Rubus* too shows an enhanced growth, the arching stems attaining a length of 1-2 ft., but the shoots of *Rubus* are not dense upon the ground so that the shade they cast is insufficient to interfere seriously with the growth of young beech and ash. Occasionally *Rubus* was found to attain a length of 3 ft. and yet be very poorly represented in number of individuals. The light values were clearly sufficient for more extended growth and we must regard *Rubus* in such cases as simply in process of invading the gap. Here too we find *erect* ash plants, their height and rate of growth depending on the size of the break in the canopy. The young beech also shows a greater degree of luxuriance, but as all under observation were eaten off it is difficult to say how long they will survive. One case was noticed, however, in the *Rubus* stage where the space was occupied by a number of beeches 20-30 ft. tall, whose stems were obliquely inclined toward the centre, and whose crowns were table-topped by reason of the lateral extension of the adjoining parent crowns. Thus the beech even in these gaps finds difficulty in permanently establishing itself so long as the general canopy of the forest is maintained.

The abundant *Rubus* which showed in gaps during 1921 was found in 1922 to have died out in some and to have been almost obliterated in others and had not yet re-appeared in 1923. This evidence shows that light intensity is not

the only important factor in the development of the flora of gaps and the conclusion seems warranted that the drying out of the soil is an important factor limiting the growth of plants in sere 2 woods.

#### *Rubus Stage.*

Here, the canopy of the trees, which appear to have attained their maximum height, has opened out slightly, permitting a more luxuriant ground flora to flourish. Only one example of an old standing wood came under my observation, viz., Charlton Old Forest, where the trees have attained an age of from 130 to 140 as determined by a count of the annual rings of felled trees. In these cross sections the last 20 rings show a very poor diameter increment, possibly indicative of the initiation of a process of decline. Jolyet<sup>1</sup> gives the maximum age attained as about 200–250, but states that the longevity varies with the altitude, and “on the banks of the Loire, it perishes in close canopy before the age of 150.” Boulger<sup>2</sup> quoting continental opinion says that “its life in a crowded wood does not often extend beyond 150–200 years.” If these continental observations are applicable to British conditions then we are here dealing with a wood which is approaching the age-limit.

*Tree-layer.* The number of stems per 100 feet square has now decreased to 22, of which 21 are “dominant” and 1 dead (Table I, column 10). The beech has apparently already attained its maximum height during the late *Oxalis* stage, for the average height in the *Rubus* stage is in the neighbourhood of 100 ft. Parts of this forest, particularly along the crest of the Down belong to sere 3 and here the height attained is much less (85–94 ft.). The trees are remarkably uniform, with about 60 ft. of the bole clear of branches, the latter ascending obliquely and supporting a foliage canopy which permits the passage of a fair amount of light.

Although neither oak nor ash occurred in the plot measured both are occasional constituents in this stage of the woodland. Both species appear “drawn up” with stems slender in comparison with the adjoining beech, e.g. an ash girthed 3 ft. 9 ins. and an oak 3 ft. 6 ins. compared with an average of 4 ft. 10 ins. for beech. A noticeable feature in this wood is the proportionately large number of deaths among the ash trees that have maintained themselves through the *Oxalis* stage. This does not seem in all cases to be due to suppression as the beech has already attained its maximum height, but possibly to the natural age limit on this soil having been reached. The last stage then consists of an almost pure beechwood, *Fagus sylvatica* having overcome many of its competitors during the Bare stage in virtue of its rate of growth and shade bearing capacity and completing the victory by reason of its greater longevity.

*The Shrub-layer.* The colonisation of gaps by *Rubus* during the *Oxalis* stage indicate the capacity of this plant to spread when conditions become suitable. The persisting individuals of the *Oxalis* stage act as centres of propaga-

<sup>1</sup> *l. c.* p. 128

<sup>2</sup> *Quart. Journ. Forestry*, 1, 1907, p. 250.

ion, and in the *Rubus* stage a definite shrub layer is formed. This shrub layer is not generally associated with beechwoods and I am informed by Mr Hobart-Lampden that on the Chilterns foxhunters are agreeably surprised to find much suitable cover under the shade of beech. The presence of *Rubus* determines the facies of the undergrowth, although it is absent from certain circumscribed areas where *Hedera* and *Oxalis* are dominant. *Rubus* attains an average height of 18 ins., with arching stems and green leaves, and for the most part forms a continuous cover, whose shade added to that of the beech canopy checks the growth of herbaceous species. It flowers and occasionally produces fruit which consists, however, of only a very small number of drupels.

The degree of luxuriance of *Rubus* seems to be chiefly determined by at least two factors, viz., light and soil moisture. The effect of the influence of these two factors cannot readily be dissociated under natural conditions<sup>1</sup>, e.g. *Rubus* attains a greater degree of luxuriance in gaps where the light supply is increased but where also competition with the roots of neighbouring trees is reduced. Even a comparison of the luxuriance of *Rubus* for the years 1921 and 1922 does not allow of a definite conclusion being drawn, for the drought of the former year is associated with much sunshine and the wetness of 1922 with much cloudiness. During the summer of 1921 *Rubus* grew luxuriantly and formed a well-defined layer but in the following year the development of the shrub layer was much less marked, the plants showing very stunted growth, many dead stems, and leaves of a pale green colour. Part of this effect may in addition be due to the effect of rabbits, which, pressed through scarcity of food, ate off the tips of the *Rubus* stems during the winter months. Nevertheless the retention of a similar vigour in the *Rubus* stage of sere 1 with a light intensity of 1/38, and the association of diminished frequency and vigour and a light intensity of 1/21 in the *Rubus* stage of sere 3 indicate that factors associated with greater soil depth play the paramount rôle.

The holly is a prominent constituent. On the shallower loams it may form a tree up to 25 ft. in height with straggling branches and relatively few leaves, but in the more typical parts it is an occasional to a frequent constituent, forming either a small tree, 4-5 ft. in height, or a low bushy undergrowth with procumbent and prostrate stems and attaining a height of 1-2½ ft. Its own canopy added to that of the beech excludes most of the herbaceous species and it permits the growth of mosses.

The ivy is locally dominant on the ground but also climbs the beech, forming one of the worst plant pests with which foresters have to contend in these woods. In the *Rubus* stage very few trees are without it. The stems, however, are cut periodically so that the canopy is little affected.

<sup>1</sup> Fricke, "Licht und Schattenholzarten ein wissenschaftlich nicht begründetes Dogma." *Verh. d. f. Gesamt. Forstw.* 30, 1904, p. 315. Burns, *Vermont Agr. Exp. Stn. Bull.* Nos. 178, 1, 193.

Among the other shrub constituents some appear for the first time such as *Cornus*, *Corylus*, *Crataegus*, *Hypericum androsaemum* and *Ribes grossularia*, and those others, recorded from the *Oxalis* stage, here show for the most part an increased frequency and enhanced growth. Their presence, however, does not appreciably affect the general facies of a matrix of *Rubus* studded with *Ilex*.

My attention has been called by Mr Tansley to the number and luxuriance of the individuals of evergreen species on the S. Downs. Brockmann<sup>1</sup> in his description of the natural woods of Switzerland remarks on the prevalence of such evergreens as *Ilex aquifolium*, *Buxus sempervirens*, *Hedera helix* and *Laurus nobilis* and adds that these show in their distribution distinctly oceanic characters. *Ilex* has an oceanic distribution and its frequency under beech (in seres 2 and 3) on the South Downs as contrasted with its occasional occurrence in scrub may be attributed to the provision of the necessary local climatic environment. Holly is also a prominent shrub in the beech-holly woods of Corsica<sup>2</sup>, but Braun does not record it from the beechwoods of the Cevennes although they form an "*îlot de végétation boréal (qui) correspond à un îlot climatique de caractère presque océanique*".<sup>3</sup> The mildness of the climate at Goodwood is emphasised by the presence of magnificent cork-oaks (*Q. suber*) growing near Goodwood House. Two trees attain a height of 48 and 53 ft., and a girth at 3 ft. from the ground of 11½ and 11¾ ft. respectively. The circumference of the area covered by the branches is 180 ft. in the former and 220 ft. in the latter. With regard to this latter tree, it is "without doubt the finest cork-oak in the South of England. It is of remarkable vigour, and in the autumn and early winter of 1911 (following the hottest summer on record) two crops of acorns were taken from this tree. The acorns of the first crop were brown in colour and of abnormal size—many of them measured 1½ ins. in length<sup>4</sup>."

Young beech and ash occur throughout the wood, the former sometimes attaining under the prevailing canopy a height of from 2–4 ft., but is of very limited occurrence and table-topped. Younger beech are comparatively infrequent and from an analysis of their height growth per annum clearly show that conditions are adverse to their growth, producing as they do the arched stem with characteristic leaf mosaic of leader and branches—a feature not found in beech growing in the open. This feature, often referred to as a direct adaptation on the part of the beech to secure the maximum light available, can be used as an index of an environment providing less light than is required for optimum development. Data giving the average annual growth of a number of 5-year old plants are recorded in Part I, and show, even under the improved light conditions, a rate of growth about 1/7 that of a plant grown in the open.

<sup>1</sup> *Die nat. Wälder der Schweiz*, 1910, p. 174.

<sup>2</sup> Rübel, *New Phyt.* **11**, 1912, p. 55.

<sup>3</sup> *Les Cevennes méridionales (Massif de l'Aigoual)*, 1915, p. 206.

<sup>4</sup> *Trees of Interest at Goodwood*, 1912, pp. 21 and 22.



Young ash is of frequent occurrence. Some are erect up to 18 ins. in height and 26 years of age, but many have prostrate stems from which arise roots and erect shoots. These at first sight appear as young plants, but when pulled up the three or four apparently separate individuals are found to belong to one stem. It was impossible to obtain the age of these either by a count of the annual growths in length or by a cross-section. Many indeed have been cut over and produced new leaders, whilst others, after attaining a certain height, have died back and produced new shoots from near the base. Clearly, although conditions allow of the ash attaining this age, regeneration is impossible and it is problematical whether, given sufficient light, these suppressed plants would ever develop into trees. On the other hand Jolyet<sup>1</sup> says in reference to beech that "les semis de cette essence se maintiennent en excellent état de végétation pendant de longues années sous le couvert de la coupe d'ensemencement, un peu diminué cependant par les coupes secondaires conduites avec prudence."

*Ground flora.* As compared with the *Oxalis* stage there is a considerable increase in the number of herbs, those common to the two stages, showing for the most part an increased frequency and enhanced growth. The newcomers have, however, a low frequency, with the exception of *Ajuga reptans* (o.-l.f.), *Asperula odorata* (l.f.), *Melica uniflora* (o.-f.-l.a.) and *Deschampsia caespitosa*, which is locally abundant near forest tracks and occasional throughout the wood. Both *Viola sylvatica* (agg.) and *Oxalis* show a slight reduction in frequency. The latter plant is sometimes locally dominant (as is also *Hedera*) and such areas may be interpreted as cases where *Rubus* has not yet completed its migration. Soil borings were made to determine the depth of loam, but this seemed quite adequate for *Rubus* growth. Attention may here be directed to the fact that some individuals of *Oxalis* were flowering at Easter 1923 and were noted as being in a more advanced state vegetatively than in the *Rubus* ages of seres 1 and 3.

Mosses similarly show an increase in number of individuals, which may partly be due to increased illumination but partly to the fact that at this age the leaf litter does not lie so thickly upon the ground. All the tree stems are covered with a thick mantle of bryophytes.

*The Effect of Wind on the Subsidiary Flora.* The southern part of the forest was felled some years ago, thus exposing the lower margin of the standing wood to the effect of the prevailing winds. The ground has been swept bare of swards for some 100 yards or more into the wood and it is of interest to compare the vegetation in the interior of the wood with that subjected to the direct and indirect effects of exposure to this new factor. The following is a list of the species observed on the exposed ground.

<sup>1</sup> l. c. p. 132.

Woody Plants.		Herbs.		Mosses.	
<i>Crataegus monogyna</i>	r.—o.	<i>Asperula odorata</i>	r.	<i>Brachythecium rutabulum</i>	o.
<i>Hedera helix</i>	r.—l.a.	<i>Dryopteris filix-mas</i>	o.	<i>Catharina undulata</i>	o.
<i>Ilex aquifolium</i>	o.	<i>Epilobium montanum</i>	o.—m.a.	<i>Dicranum scoparium</i>	o.
<i>Lonicera periclymenum</i>	o.	<i>Geranium robertianum</i>	r.	<i>Eurhynchium praelongum</i>	a.
<i>Rubus fruticosus</i> (agg.)	a.	<i>Hypericum pulchrum</i>	r.	<i>E. striatum</i>	o.
<i>Ruscus aculeatus</i>	r.	<i>Luzula pilosa</i>	o.	<i>Fissidens taxifolius</i>	o.
<i>Viburnum lantana</i>	r.	<i>Melica uniflora</i>	r.	<i>Hylocomium loreum</i>	o.
<i>V. opulus</i>	r.—o.	<i>Milium effusum</i>	o.	<i>H. triquetrum</i>	o.—f.
		<i>Oxalis acetosella</i>	o.	<i>Hypnum cupressiforme</i>	o.—l.d.
		<i>Senecio jacobaea</i>	r.	<i>Isoetium myurum</i>	o.
		<i>Veronica officinalis</i>	r.	<i>Polytrichum formosum</i>	o.
		<i>Viola sylvatica</i> (agg.)	l.	<i>Thuidium tamariscinum</i>	o.—f.

Much of the ground is bare and incompletely colonised, due not only to the small number of individuals present but to the elimination of many species found in the interior of the wood. And this reduction is not compensated for by the appearance of *Epilobium montanum*, *Hypericum pulchrum*, *Senecio jacobaea* and *Veronica officinalis*—the occurrence of the first three being no doubt due to the increased lateral illumination. The reduction in the frequency of the survivors is somewhat accentuated by their small size. *Rubus*, although still abundant, has an average height of about 9 ins., having few stems and pale green leaves. The individuals are isolated and the stems of neighbouring plants do not intertwine. *Oxalis* is occasional only, although small groups sometimes occur, but all plants show small leaves. *Melica* is represented by one tiny plant and *Viola* is now local.

Thus exposure to wind and increased illumination, by increasing transpiration, by the removal of leaf litter and the drying out of the soil, disturb the conditions favouring the growth of these woodland plants and the evidence indicates the dependence of *Rubus* and *Oxalis* upon an adequate water supply and the inability of the soil supporting the consociation (sere 2) to supply this for the good growth of these plants in the absence of sheltering woodland.

#### THE BEECH CONSOCIATION OF SERE 3.

The later stages of the consociation in sere 3 are well represented, but only one small area was discovered which corresponded in age to the Bare stage of the previous seres.

##### Bare Stage.

*Tree Layer.* In the unit area there are 208 stems of beech and 176 of ash. In this case the crown strata were not classified but a felled ash, 45 years of age, measured 52 ft. and the beech had outgrown it. The ground was littered with dead stems of beech and ash, but chiefly the latter. No oak was observed.

*Ground flora.* The subsidiary flora is conspicuously lacking in higher plants. *Rubus* is absent, whilst ash seedlings are rare. Herbs are represented by the rare occurrence of *Viola sylvatica* (agg.). Mosses are relatively well represented.

##### Late Bare Stage.

This refers to woods from about 80–100 years old, in which the essentially bare floor of the younger woods is maintained.

*Tree-layer.* Woods 12 and 13 show a relatively dense stocking of beech (44 and 37 trees per 100 feet square respectively) but compared with woods of similar age in sere 2 (7, 8 and 9) the trees show a smaller girth. In wood 12 with a northern aspect the beech measured 95 ft. in height and in wood 13, a marginal tree measured 100 ft., but those in the interior were estimated at about 90 ft. No ash was seen in either of the woods, but the oak is occasional.

The herbaceous vegetation is similarly poor in species and in individuals and is insufficient to interfere with the general impression of a bare forest floor. It is of interest to note, however, the occasional local dominance of *Hedera* and the local abundance of *Oxalis* in one wood. In gaps the following additional species make their appearance: *Ajuga reptans*, *Asperula odorata*, *Circaea lutetiana*, *Geranium robertianum* and *Sanicula europaea*.

Mosses are well represented in species but have a very low frequency.

### *Rubus Stage.*

This stage was shown by one wood, part of which (the southern portion) had a loamy soil covering, whilst the major portion had a calcareous soil. It thus shows certain characters transitional between seres 2 and 3. A count of the rings of cut stumps shows a variation in age from 130–150.

*Tree layer.* The total number of "dominants" is 21, composed of 19 beech and 1 each of oak and ash. The girth of the ash is 2 ft. 11½ ins., the average of two oaks 3 ft. 2 ins., compared with 4 ft. 9 ins. for beech. These data demonstrate the slender character of the oak and ash stems. The beech in the southern portion varied in height from 86 to 98 ft.,—the average of four measurements giving a height of 94 ft. In the calcareous part of the wood, where the total depth of exploitable soil is about 24–30 ins., the height of the beech is from 85 to 90 ft. The ash tree included in the sample plot is associated with oak, this species not being generally distributed throughout the wood.

*Shrub layer.* In the southern part of the wood, where the soil has a covering of loam up to 12 ins. in depth, the subsidiary vegetation is better developed than in the rest of the wood. The higher frequencies are generally recorded from this part.

On the loam *Rubus* attains a height of about 12 ins. but does not cover the ground so completely as in sere 2. On the calcareous soils the plants are wider apart, from 8–9 ins. tall, and with pale discoloured leaves. The abundance of *Ilex* is a noteworthy feature of this wood. Along the southern margin it is much more robust with many more leaves than in the calcareous part of the wood, where it is sometimes locally dominant, but is a straggly plant with comparatively few leaves. It is however always erect, the procumbent forms which are conspicuous in sere 2 being very rare here. No seedling beech was observed and young ash is of occasional occurrence only. One seedling of *Castanea sativa* was recorded in 1922.

*Ground flora.* In the list of herbs the higher (and local) frequency is recorded from the southern portion, whilst much of the ground in the rest of the wood is bare, showing however the same species but with a low frequency and small size.

Throughout the major portion of the wood *Oxalis* is represented by scattered individuals, but along the brows of terraces and in the neighbourhood of tracks, which are of insufficient width to influence the canopy, it becomes frequent. In the southern portion it is abundant. *Oxalis* is sometimes associated with *Thuidium tamariscinum*. This association has been frequently observed in gaps in the ash-oak zone of woodlands on a N.-facing calcareous slope in Stead Combe to the S.W. of Cocking. Indeed *Oxalis* was not observed here apart from a mossy carpet.

Mosses also show a somewhat reduced frequency. The tree stems are again covered with a mantle of bryophytes.

#### THE BEECH CONSOCIATION IN OTHER AREAS.

##### *South Downs.*

*West Dean Estate.* To the west of the Goodwood estate, lies the estate of West Dean. Most of the woodlands there are coppiced forms of the ash-oak associates, but planted even-aged beechwoods occur. The application of the system of classification adopted for the Goodwood area shows that one wood belongs to sere 3, another (recently felled) to sere 2, whilst a third, of somewhat varied character, is most nearly related to sere 3.

*Ditcham Park Estate.* The beechwoods on this estate are classified by Adamson into the "beechwoods on the chalk," and the "beechwoods on the plateau." The former are relegated to sere 4. It is doubtful if the latter have grown up under conditions comparable to those obtaining at Goodwood. *Oxalis* is recorded only as a rare plant from one of the woods, but it is of interest to note the luxuriance of "abundant" *Rubus leucostachys* (with frequent *R. rusticanus*) in one of the woods and its local abundance in the two others described. The general description regarding the shrub layer and the ground flora suggests the relegation of two of the woods to sere 3 and one to sere 2.

##### *Cotteswoldes.*

The succession of plant communities described in Section I is not nearly so obvious on the Cotteswoldes nor on the Chilterns, for in both areas, enclosure with intensive grazing and cultivation sets definite limits to woodlands. In neither of these areas have the woodlands been examined in detail. On the Cotteswoldes the plateau beechwoods are isolated, often mixed with oak, and in many cases of small extent with a composite ground flora. In one locality common land has been invaded from the escarpment beechwoods and now bears a wood with trees about 45 ft. tall growing on a sticky loam 16 ins. deep. Most of the trees have more than one stem. The ground flora is similar to the *Oxalis* stage with *Oxalis*, a., *Viola sylvatica*, a., *Deschampsia caespitosa*, o.,

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*Ajuga reptans*, l.f., *Asperula odorata*, and *Carex sylvatica*. *Rosa arvensis* and *Rubus fruticosus* (3-6 ins. tall) also occur. The above suggests the sequence observed on the South Downs.

### *Chilterns.*

In the beechwoods on the Hampden estate selected trees are cut and manufactured on the spot. The woods are for the most part even-aged and contain many oaks among the beeches, which, from the cut stumps, appear to grow more slowly than the beech of sere 2. The following details of the girth and height of four beeches of sere 0 were kindly supplied by Mr Hobart-Hampden.

(1)	Circumference at breast-height	3 ft. 1 ins.;	height 63 ft.
(2)	"	"	3 ft. 10 ins.    "    70 "
(3)	"	"	3 ft. 5½ ins.    "    78 "
(4)	"	"	5 ft. 2½ ins.    "    85 "

Beech trees on the South Downs with similar girths attain a much greater height.

The *Oxalis-Rubus* sequence has not been observed, but in the gaps a core of *Rubus* with peripheral *Oxalis* may occasionally be seen, in one wood with a meagre ground flora. In older woods, *Rubus*, which is a prominent and often dominant plant, is frequently accompanied by a vigorous growth of tall grasses—*Deschampsia caespitosa*, *Festuca gigantea*, *Milium effusum* and *Elymus europaeus*. *Polytrichum formosum* is also prominent. Among the plants not recorded from Goodwood are *Holcus mollis*, *Stellaria holostea*, *Elymus europaeus* and *Luzula multiflora*. Mention may also be made of the fact that under isolated beech occur *Holcus mollis*, *Deschampsia flexuosa*, *Festuca ovina*, *Agrostis tenuis* and *Poa pratensis*—forming a plant covering similar to that in some beechwoods in the north of Scotland. Such an assemblage of plants has not been observed either on the South Downs or on the Cotteswoldes.

### DISCUSSION AND INTERPRETATION OF RESULTS.

Comparison of the beechwoods belonging to the different seres is rendered difficult for a number of reasons. In the first place the number of adult woods examined is limited and the mature wood of sere 1 has not been seen. Then sere 4 has not been investigated from the standpoint here adopted and the presence of non-woodland species in Adamson's lists indicates that we are not dealing with a wood with a continuous canopy as in the beechwoods at Goodwood, which also cover large areas and whose flora is not influenced by lateral illumination. Finally the Chiltern woods belonging to sere 0 have not been investigated in sufficient detail to permit of close comparison. Attention will therefore be directed to salient points and inferences made by contrast of the extreme seres.

We are dealing with woods whose soils through leaching form a series with respect to such soil factors as depth of loam, acidity, humus content, texture

and presumably water content. The various complexes of factors are accompanied by changes in the flora, whose variations in species occurrence, frequency and degree of luxuriance may be related to these.

We may note in the first place the essentially herbaceous facies of the subsidiary flora in sere 4, where *Sanicula*, *Ajuga*, *Viola silvestris*, *Euphorbia amygdaloides*, *Asperula odorata*, *Mercurialis perennis* and *Lamium galeobdolon* are the prominent plants. In sere 0 the herbaceous facies is obscured by conspicuous *Rubus* and tall grasses, among which *Deschampsia caespitosa* and *Milium effusum* are the most important. This change is already noticeable in sere 2 where *Deschampsia* is locally abundant, and the occasional occurrence of this plant in the immature woods of sere 1 seems to indicate that it will play a conspicuous part in determining the facies of the mature wood.

Prominent among the plants present in sere 4 but absent from sere 0 are: *Clematis*, *Cornus*, *Euonymus*, *Ligustrum*, *Cephalanthera grandiflora*, *Mercurialis perennis* and *Viola hirta*, whilst *Luzula pilosa*, *Oxalis acetosella*, *Holcus mollis*, *Milium effusum*, *Poa trivialis*, and *Stellaria holostea* are absent from sere 4 and present in sere 0. The flora of sere 0 still retains many species more generally associated with basic soils but the typical calcicolous facies is lacking. The presence of such species as *Holcus mollis*, *Digitalis purpurea*, *Luzula multiflora*, *Hypericum pulchrum* (the last three recorded from a large gap and not included in the list) emphasise the acidic tendency. Comparison of the oak consocieties with the oakwoods on siliceous soil cannot be made because the former are undergrown with young beech and the subsidiary flora to all intents and purposes is that of a beechwood which has not yet reached maturity, but the available evidence seems to relate the flora to the dry facies of the damp oakwood.

The hornbeam (*Carpinus betulus*) has been observed in pre-climax woods on the Chilterns but apart from hedgerows, where it is probably planted, it has not been seen on the South Downs.

Variation in frequency is often accompanied by alteration in the degree of luxuriance. In sere 4 the oak is a rare plant, whilst in sere 0 it is an occasional to a frequent constituent. Owing to the lack of definite data it is not known whether the increased competitive power of the oak is due solely to enhanced growth or to a falling off in the competing ability of the beech, for as already pointed out beech appears to grow more slowly on the Chilterns than on the South Downs. Possibly both factors are operative. Young sapling oaks are much more common in gaps in sere 0 woods than in any of the other seres. The competing power of the ash seems definitely to have reached its maximum under the complex of factors present in sere 1, for as already pointed out it holds its own with beech for a progressively longer time as we pass from sere 4 to sere 1. On the Chilterns however ash is not represented in the oak consocieties nor in the beech consociation of sere 0. Young ash plants, slow grown like those in South Down beechwoods, were observed as occasionals in one beechwood,

and ash is a locally dominant plant in the seral stages observed on common land (the depth of the loam was not determined). It may be mentioned here that ash was absent from some sheltered valley slopes where it would have occurred in such situations on the South Downs, but was observed locally abundant in gaps in a plateau wood showing affinities with sere 3. The above observations are in keeping with its known distribution in oakwoods, where it is abundant in the basic or neutral damp oakwood but is absent from the acidic dry oakwood and suggest that progressive leaching of the chalk has ultimately brought about conditions hostile to ash growth.

Increased frequency and enhanced vigour of *Rubus fruticosus* (agg.) go together as we pass from sere 4 to sere 0. In sere 4 this plant makes an unimportant contribution to the subsidiary flora. In sere 3 it is abundant to locally dominant—the latter frequency being recorded from soils with a covering of loam. Where the soil is shallow and calcareous, *Rubus* is less abundant and less luxuriant and throughout the mature wood of sere 3 is on the whole a rather *chétif* straggling plant rising to an average height of about 9 ins. In sere 2 the plant forms for the most part a continuous cover, is more robust, with greener, healthier looking leaves and attains an average height of about 18 ins. In sere 1, in the immature wood described, *Rubus* does not cover the ground quite so well as in sere 2 but the general vigour is maintained if not surpassed, and it seems reasonable to suppose that with further reduction in the number of trees, *Rubus* would attain a more robust and luxuriant growth. In some parts of the Chiltern plateau woods the most vigorous and healthy looking *Rubus* was observed—this plant forming a formidable obstacle to beech regeneration. It is thus evident that growth conditions become progressively more favourable as we pass from sere 4 to sere 0.

The holly is an associate of the oak on drier soils, and this is confirmed by Salisbury<sup>1</sup> for the Hertfordshire woods where it is more commonly found in woods of *Quercus sessiliflora*. It occurs in all the climax beechwoods. In sere 4 Adamson records it as occasional, but locally very abundant in Head Down Hanger. In sere 3 it is abundant to locally dominant—the latter frequency on thin loams, where the shrub is also more luxuriant than on calcareous soil, on which the plants are straggling and have few leaves. In the mature wood of sere 2 *Ilex* typically forms low dense undergrowth. A similar growth form has been observed in the *Oxalis* stage of sere 1, in the *Rubus* stage of which it is occasional to frequent. In sere 0, apart from its local dominance in one wood, it is only occasionally found. The above record of its distribution again emphasises the preference of *Ilex* for permeable soils.

Other plants, chiefly tall grasses, show (on the Chilterns) increased frequency combined with more vigorous growth. Prominent among these are *Deschampsia aespitosa*, f.-d., *Festuca gigantea*, o.-l.a., and *Milium effusum*, f.-l.d. With these may be mentioned *Pteridium aquilinum*, which is occasional to locally

<sup>1</sup> This JOURNAL, 4, 1916, p. 49.

dominant in sere 0 woods. On the other hand *Brachypodium sylvaticum* shows a reduced frequency.

Some inquiry may now be made into the causes of the occurrence of *Oxalis* as recorded in these woods. As previously pointed out, there is no correlation between the observed distribution of *Oxalis* and the light intensity, and this, at least in seres 2 and 3, is not the factor determining the Bare soil-*Oxalis*-*Rubus* development. Again the low acidity of the seres with calcareous soils cannot be considered as limiting to *Oxalis* for this plant grows luxuriantly in wood 7 on a soil with a pH of 7.1. The higher pH values (up to 8.5) may conceivably be limiting to *Oxalis*, but a pH of 7.5-7.9 is not<sup>1</sup>.

To explain the distribution of *Oxalis* the hypothesis is advanced that soil water content is the deciding factor. Whilst this has not been submitted to the test of experiment the following observations seem to establish a reasonable possibility that this is so.

We may remind ourselves that the calcareous soils of sere 4 are shallow and permeable and occur on slopes with a rapid run off, and that as we pass from sere 4 to sere 0 the total depth of soil increases. This is generally (although not necessarily) accompanied by an increase in depth of loam, whose texture also becomes closer and more compact. The deeper and less permeable soils will have a more eustatic water content, being less liable to dry out than the shallower and more permeable soils. Further, on the shallower soils the beech roots are necessarily limited to the superficial layers, where root competition will be keener than on the deeper soils with a larger exploitable volume at the disposal of the accommodating root system of the beech. In this connection reference may be made to the finding on p. 45, where from a study of the behaviour of ash and beech in mixture it was concluded that competition was keener on the shallower soils.

On this hypothesis the absence of *Oxalis* from sere 4 is attributed to the lack of suitable water conditions and the frequent association of this plant with a carpet of *Thuidium tamariscinum* on a north-facing valley slope suggests that the mossy carpet induces conditions which permit of *Oxalis* survival and growth. Again the appearance of *Oxalis* in seres 2 and 3 is believed to be delayed until such time as the root competition of a diminishing number of trees becomes progressively less severe until a point is reached when *Oxalis* can establish itself. Thus *Oxalis* occurs in sere 1 when there are 200 stems per 100 sq. ft., in sere 2, 32 to 48, and in sere 3 when the number is reduced to 24. This is supported by the fact that *Oxalis* occurs in gaps whilst it may be absent from under a continuous canopy where the light intensity is above the minimum for *Oxalis*. Observations of a like character point to a similar conclusion, e.g. the occurrence of *Oxalis* along the brows of terraces where the soil is deeper, in forest tracks where the cart wheels have severed the beech roots, and occasionally at the bases of trees where the soil is better watered from the accumulated rain running down the tree trunks.

<sup>1</sup> Olsen. *Compt. rend. d. Trav. d. Lab. Carlsberg*, 15, 1. 1923. n. 82.



In support of this contention, reference may be made to the response made by *Oxalis* to the removal of beech root competition by digging a trench which severed the beech roots round a small area<sup>1</sup>. When examined in April 1920 following the cutting of the trench the *Oxalis* inside the area showed much earlier development with expanded leaves and numerous flowers, whilst outside, the leaves were still folded and few flowers observed. In July of the same year the differences related chiefly to the slightly greater size of the leaflet and its deeper green colour inside the enclosure than outside. These observations indicate that *Oxalis* had benefited by the absence of beech root competition. Similar results were obtained at Craibstone where outside the enclosure *Oxalis* was represented by rare and puny individuals whilst inside it showed vigorous growth and was accompanied by other plants which appeared for the first time.

In these experiments at Goodwood the areas were enclosed by a wooden framework, extending about 9 ins. above soil level, and covered by wire netting of  $\frac{1}{2}$  in. mesh. This excluded the annual fall of leaves, so that by 1923 the leaf litter in the enclosure had practically disappeared. In that year the following notes were made upon *Oxalis*. At Easter in the control plot (not surrounded by a trench) there appeared only three small leaves of *Oxalis*, whilst in the other plot (surrounded by a trench) *Oxalis* was recorded as frequent and further advanced vegetatively than outside the area. In August, in the control plot there were only 10 leaves showing with an average diameter of  $\frac{1}{2}$  in. In the "trenched" plot there were 200 leaves with diameters varying from  $\frac{1}{4}$  to  $\frac{3}{4}$  in. whilst outside the leaves were variable but up to  $1\frac{1}{4}$  in. in diameter.

In both the plots mentioned there has eventually been a very marked decline both in number and degree of luxuriance of the *Oxalis* plants; but this is most apparent in the control plot. The interesting point brought out in the later stages of the experiment is the apparent correlation between the disappearance of the leaf-litter and the reduced number and vigour of *Oxalis*. Similar observations have been made elsewhere. For example, in the grassy beechwoods on siliceous soils, *Oxalis* is a rare and tiny plant in those parts where *Deschampsia flexuosa* is dominant. From these parts the beech leaf-litter is blown away by the wind. Where *Holcus mollis* is dominant the beech leaves accumulate and there *Oxalis* is a luxuriant and sometimes a very abundant plant. Again, reference may be made to the wind-swept southern margin of Charlton Forest, where the reduction in frequency and degree of luxuriance of *Oxalis* has already been pointed out. The foregoing observations and experiment demonstrate the importance of leaf-litter to the welfare and

<sup>1</sup> This experiment was originally designed to exclude rabbits, birds, etc., and plots were surrounded by wooden frameworks and covered with wire netting. Round one of the plots a trench (subsequently refilled) was dug. The *Oxalis* in the control plot was less luxuriant than in the area surrounded by the trench. The enclosing boxes do not seem to be in any way responsible for the observed changes in the luxuriance of *Oxalis* inside the enclosed plots.

survival of *Oxalis*. The time of appearance of *Oxalis* in the different seres of the Goodwood area cannot be correlated with the leaf litter because this is of practically uniform depth throughout.

The evidence from the occurrence and degree of luxuriance of *Rubus* also supports the water supply hypothesis. Here again there is no obvious correlation between light intensity and the presence and vigour of *Rubus*, which shows similar dwarfing in the Bare stage of sere 1 (light intensity 1/37) and the Late Bare stage of sere 3 (1/22). On the other hand, as previously pointed out, there is a correlation between soil depth and the degree of luxuriance attained.

That soil water content is the deciding factor seems indicated by the above relation and is supported by observations on the behaviour of *Rubus* after the dry summer of 1921<sup>1</sup>. For example, *Rubus* was recorded in 1921 as co-dominant from some gaps in wood 9 (sere 2) but was barely noticeable in the following summer; and in a gap in the *Rubus* stage of the same sere, the position of dominance had been attained by *Rubus*, under the shade of which a light intensity of less than 1/100 was obtained, but in 1922 the shade cast by the straggling stems was quite insufficient to prevent the growth of herbaceous plants. Additional support is lent to the above by the reduction in frequency and size of the plants in the wind-swept zone of Charlton Forest.

These observations relating to *Oxalis* and *Rubus* apply generally to the associated species of the ground flora and suggest that the chief factor responsible for the recorded floristic differences is the soil water content. In sere 0 other factors, such as acidity, deficient soil aeration and soil texture may assume critical importance.

#### SUMMARY OF SECTIONS II AND III.

In Section II, the *modus operandi* of beechwood reproduction is described.

Some preliminary remarks are made regarding beech mast production in this country. Full mast years occur at irregular intervals, during which partial crops occur, but the depredations of animals upon the nuts and seedlings tend to limit successful regeneration to years of full crop.

The beech is a heavy seeded tree and the wind as a dispersal agent is operative only where it has free play. In beech high forest the nuts as a rule drop vertically downwards.

Under existing conditions seedlings survive only in gaps where young beech forms a zone peripheral to a central area occupied by a variety of plants. These gap floras are analysed and the species, species frequency and degree of luxuriance are correlated with the size and age of the gap and the age of the beechwood when the gap was formed. The relation of this gap flora to beech seedling survival is discussed.

When the formation of a gap coincides with or approximates in time to a

<sup>1</sup> The annual rainfall at the nearest station (West Dean Park) was as follows: 1920, 37.32 ins.; 1921, 21.45 ins.; 1922, 37.26 ins.

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Each mast year a peripheral zone of beech frequently encloses a central core of the more mobile woody species such as ash and sycamore. If formed in intervals between mast years the gap may be fully colonised by thickets of ash, which when young are impregnable to beech, but in which in later life beech growth is rendered possible by the opening out of the ash canopy. The subsequent development of such reproduction circles is outlined.

This study of the reproduction explains the even-aged character of the different stages of the beech associates and of the beech consociation.

In Section III the structure and life history of the beech consociation are described.

The life history of the wood begins with a mixture of ash and beech. With increase in age there is a decrease in the total number of stems per unit area, relatively more ash are eliminated than beech. At certain ages varying with the different seres ash is definitely relegated to a subordinate place and the mature wood is over 90 per cent. beech.

The above changes are accompanied by changes in the subsidiary flora. At first the ground vegetation is practically absent; then *Oxalis acetosella* becomes dominant; finally a shrub layer dominated by *Rubus fruticosus* (agg.) comes into its appearance. Three stages in the life-history of the wood are thus distinguished, viz, Bare, *Oxalis* and *Rubus* stages.

Upon the basis of the time of appearance of the *Oxalis* and *Rubus* stages in the life history of the beech consociation, the South Downs plateau woods have been relegated to seres 1, 2 and 3. Adamson's "beechwood on chalk"—distinguished by the absence of *Oxalis* and a distinct shrub layer—is added to sere 4 and certain woods on the Chiltern plateaux as sere 0 (v. diagram, p. 10).

Data regarding soil depth, soil texture and hydrogen ion concentration support the above floristic separation. It is shown that light is not the only factor determining the Bare soil-*Oxalis*-*Rubus* development.

Structural details are then given of the three stages of the different consociations. In each stage the crown canopy is analysed as well as the subsidiary vegetation. The following are the most important points brought out by this analysis.

The ultimate height growth attained by beech is greater by about 10 ft. in sere 2 than in sere 3. The available evidence indicates that the height growth of beech in sere 0 is less than in sere 2, and that the best growth of beech is obtained under the complex of factors bearing sere 2 vegetation or under a balance between sere 2 and sere 0.

Ash is present as an occasional tree in the canopy of the beech consociations. It is the climax of seres 1, 2, 3 and 4 but is absent from sere 0. Despite advanced growth of beech the competitive power of the ash increases relatively to that of beech as we pass from sere 4 to 1. Pure beechwood is formed soonest in sere 4 and is delayed longest in sere 1. Thus

sere 1 provides the conditions conferring the maximum competitive powers on ash.

The data available indicate that the competitive power of the oak is increased as we pass from sere 4 to sere 0.

A definite shrub layer is not formed in sere 4, but occurs in the other four seres. This is dominated by *Rubus fruticosus* (agg.) but in sere 3 *Ilex aquifolium* is locally dominant. The degree of luxuriance attained by *Rubus* increases as we pass from sere 3 to sere 0.

Floristically the ground vegetation is similar in seres 1, 2 and 3, but varies in the time of its appearance in the life-history of the woodland. In sere 4 the subsidiary vegetation has a distinctly herbaceous and calcicolous facies and in sere 0 tall grasses are often locally dominant and the facies is decidedly more acid.

Data respecting the degree of luxuriance attained by *Oxalis*, *Rubus* and other members of the ground flora, the behaviour of these in the various con-sociations and when exposed to wind provide evidence for the hypothesis that the Bare soil-*Oxalis-Rubus* development is partly determined by root competition of the trees and that the appearance of the subsidiary vegetation is delayed until such time as root competition becomes less severe finally permitting of the establishment of a ground flora and a shrub layer.

The present work shows that certain characters of the subsidiary vegetation may be correlated with the growth of the dominant trees.

## APPENDIX.

### THE STATUS OF SYCAMORE.

Although not a native of this country, the sycamore (*Acer pseudoplatanus*) has become an established member of our woodland flora. In the woods of the Goodwood area it is not a frequent, generally distributed, tree but it is locally very abundant in the beech associates, sometimes indeed taking almost entire possession of gaps. Gaps in the woods of Denmark may be similarly occupied<sup>1</sup>. Its local occurrence is no doubt due in the first place to sporadic planting, but most of the present growth is undoubtedly subspontaneous, competing with both beech and ash. A further study of these local areas will serve to show the effect of the introduction of the sycamore and some index of its probable future place in these woods will be obtained.

The sycamore in canopy produces mobile seed abundantly and annually after it has attained 40 years of age. The seed germinates freely and the seedling is almost immune from rabbit attacks, although the sapling is liable to be peeled later. *Rhytisma acerinum* (agg.) however acts as a severe check upon seedling growth particularly under deeper shade.

In its light demands the sycamore occupies a position in the scale of

<sup>1</sup> Warming. *Bol. Tids.* 35, 1919, p. 535

tolerance between beech and ash, but is much nearer the former when adult trees are compared. Like the ash sycamore seedlings can persist where beech seedlings die, but show a slow rate of growth, attaining a height of 4-6 ins. in as many years.

With regard to its soil demands Mathieu<sup>1</sup> says that these are the same as for the beech, its "*bonne venue*" indicating a fertile soil rich in nutritive mineral elements. Although not absent from the shallower soils the sycamore is at present found most abundantly on the deeper loams of the Goodwood area.

According to the authority cited the sycamore's rate of growth in youth is rapid and at 30 its height is twice that of beech of the same age; later this rate of growth slows down and at commercial maturity the yield is much the same. With regard to the longevity of the tree Loudon<sup>2</sup> states that it is "from 140-200 years, though it has been known of a much greater age," and it "arrives at its full growth in 50 or 60 years."

Thus the sycamore is endowed with a combination of qualities which are divided between beech and ash, viz. shade bearing capacity and ease of seed dispersal combined with frequency of seed production. It thus can compete with ash for vacant ground and with beech for a place in the canopy of the mature wood.

#### *Sycamore v. Ash.*

The frequency of seed production, the age at which this occurs and the adaptations for, and the agents of, seed dispersal are very similar in these two trees. The immunity of sycamore seedlings to rabbit attack confers an advantage over the ash but like beech seedlings they do not seem to possess the recuperative capacity of this tree.

In the absence of the animal factor the success of the sycamore in competition with ash will be determined by the former's greater tolerance of shade. In a planted wood of ash and sycamore occurring in about equal proportions, with local pure consociates of each, the ash had attained a height of about 60 ft., while the sycamore formed a sub-canopy at a height of 50-55 ft., reminding one of the similar relation existing between ash and beech in the earlier stages of the development of the beech consociation. The relative capacity to bear shade may be deduced from the occurrence and height growth of certain constituents of the undergrowth, e.g. *Sambucus nigra* attains a height of 10-12 ft. under the canopy of ash, of 3 ft. under mixed ash and sycamore, whilst it is absent from the consociates of pure sycamore. The ground flora reflects similar variations.

In another wood where occur several secondary consociates of sycamore of different ages and varying in height from 25 to 40 ft., the subsidiary vegetation consisted, in the younger communities, of an occasional *Rubus* and young ash 6-7 ins. high and 4-5 years old, whilst in the older the number of species present

<sup>1</sup> l. c. 1897, p. 39.

<sup>2</sup> *Arb. et Frut. Brit.* 1, 1854, p. 416.

was greater and young ash of similar height were met with. No case has come under my observation where ash has attained any greater height than this under a canopy of pure sycamore of this age.

*Sycamore v. Beech.*

The contest between sycamore and beech presents many features similar to that between ash and beech but by reason of the greater shade-bearing capacity of the sycamore the opponents are more evenly matched. Under a sycamore canopy it is found that ash attains a greater height than under a canopy of beech of corresponding age. Again under the canopy of an oak consociation, beech, sycamore and ash formed an undergrowth, but the last, which had attained a height of 12-15 ft., had not the healthy vigour of the two former.

Now where all three trees occur, in addition to oaks, birches and elms, it is found that the gaps are filled either by a pure group of sycamores or of ash or of the two in mixture. Occasionally we find a central core of mixed ash and sycamore surrounded by a ring of beech and sycamore. Also it was observed that under a canopy of oak-ash-birch, sycamores had formed an underwood and attained a height of 40 ft. Now the planted parent sycamores had attained the same height as the older trees in the mixture so that it seems likely that the sycamore left to itself will oust the more light-demanding dominants such as birch and ash.

It seems probable therefore that, where beech, ash and sycamore occur together, the ash will to a large extent be replaced by the sycamore, which, equipped with a mobile and frequently produced seed and with a degree of shade tolerance approaching that of beech, will continue as a rival to the beech. Whether on certain soils there will be formed an association of beech and sycamore, like the beech-maple climax of eastern North America, cannot, in the absence of further observation, be definitely asserted.

In conclusion, to Mr Tansley, who, during this investigation has given me much encouragement by kindly criticism and suggestion both in the field and during the writing up of results, I am especially indebted. I have also to acknowledge with gratitude the financial assistance given by the Carnegie Trustees without which the work could not have been carried out.

# SPARTINA TOWNSENDII; ITS MODE OF ESTABLISHMENT, ECONOMIC USES AND TAXONOMIC STATUS.

By F. W. OLIVER.

(With Plate I and eight Figures in the Text.)

HAVING regard to the fact that it is fifty or more years since *Spartina Townsendii* first appeared from the unknown in sheltered waters about Southampton, it might be judged remarkable how little precise information about it has found its way into the literature of botany. It is not as though this were a rare or obscure plant with a secret locality closely guarded by the initiated. For thirty years, certainly, *S. Townsendii* has stood in the light of day, visible to every passer by, the most conspicuous feature in every landscape which it has invaded. Its spread from the point where it was originally discovered has been continuous and remarkable. First operating in its home waters, it gradually found its way on the mainland to Hurst Castle in the west and to Chichester Harbour in the east, at the same time occupying the sheltered localities along the shore of the Isle of Wight. It has since spread by natural agencies west and east along the south coast to Poole Harbour (1899), Christchurch Harbour (1913), Pagham Harbour (1918) and Rye (1921), whilst on the French side of the Channel it was reported in 1906 (Vire and Saire), and in more recent years has penetrated into the estuaries of the Seine (1915), the Orne (1918), the Touque (1922), and the Elorn, near Brest (1921). The recent rapid spread in the north of France has attracted considerable attention among botanists (Fig. 1).

The normal habitat of *Spartina Townsendii* is soft tidal mud extending not further than 3 ft. below the high-water mark of spring tides. These muds usually (perhaps always on the south coast?) carry a close felt of *Zostera nana*, and, in the absence of *Spartina*, so remain. For centuries, apart from the *Zostera*, these muds must have remained bare, till the accident of *Spartina*'s arrival provided a further and surprising next stage in the succession. With the establishment and meadowing of *Spartina*, the *Zostera* is effaced, and *Spartina* reigns in its stead. This may perhaps be a direct result of light-screening, but the matter has not been particularly investigated. It has, however, a certain importance, as the sequel will show.

At the edge of a *Spartina*-field, where the ground begins to slope down to the creek, there remains generally a zone of *Zostera* free from *Spartina* invasion. The areas of these two plants do not absolutely coincide—the *Zostera* being able to reach down a trifle lower. It may be that the conditions on these

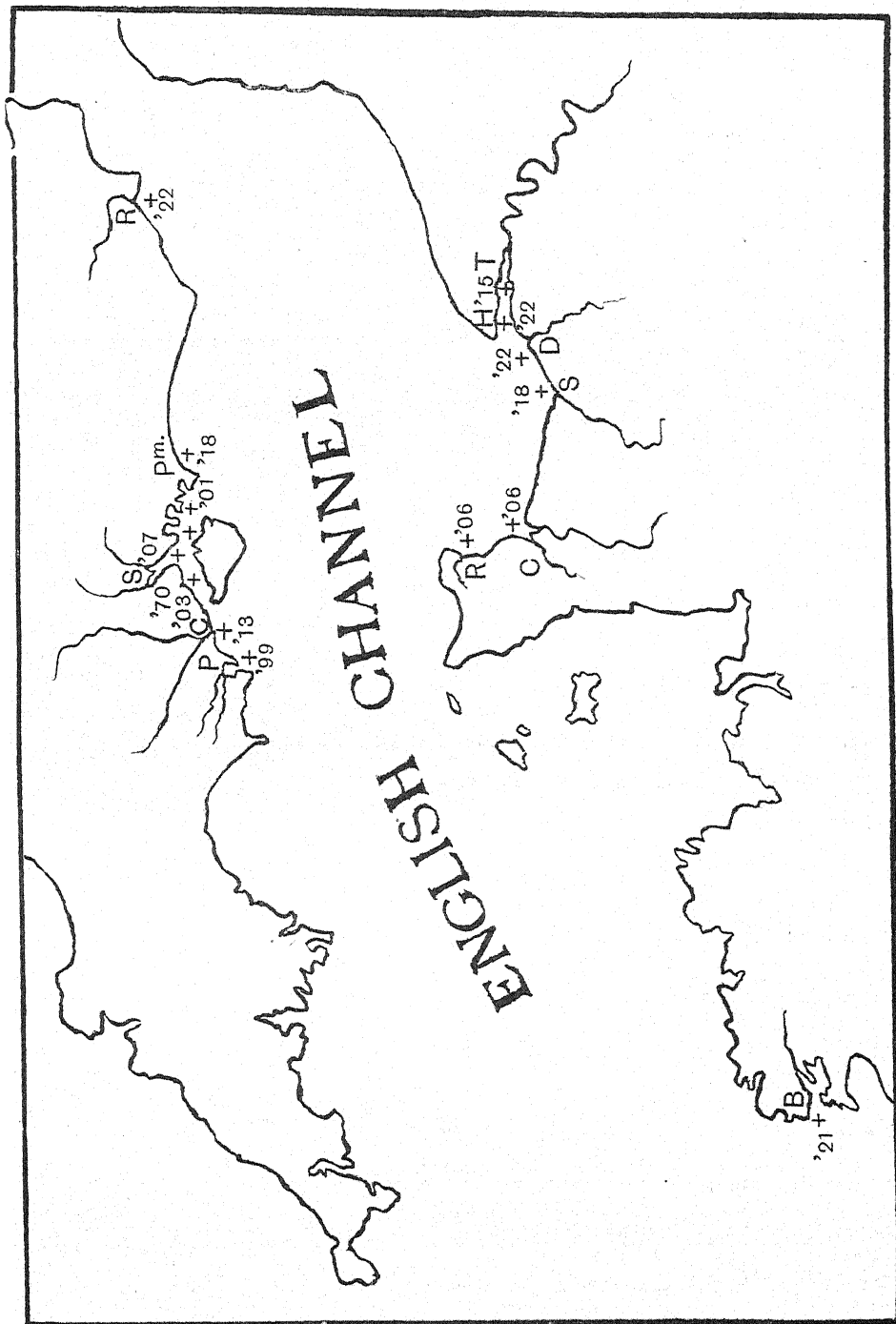


FIG. 1. Present natural distribution of *Spartina Townsendii* (+ + +) on the English and French coastlines of English Channel, with dates of first establishment. *English Coast*: P., Poole Harbour (1890); C., Christchurch Harbour (1913); S., Southampton (1870); P<sup>m</sup>, Pagham Harbour (1918); R., Rye (1922). *French Coast*: B., Brest (1921); R., Réville (1906); C., Carentan (1906); S., Sallenelles (1918); D., Deauville (1922); H., Havre (1922); T., Tancarville (1915).



slopes are unsuitable for *Spartina* in consequence of the longer period of tidal immersion. Roughly, 6 hours' immersion per tide is the limit which *Spartina* can tolerate.

Before leaving the subject of distribution it may be pointed out that in addition to the normal non-colonisation by *Spartina* of these *Zostera*-fringes there exist apparently suitable areas under *Zostera* upon which no plant of *Spartina* gains a footing. This failure to colonise is conspicuously illustrated at Poole Harbour by a number of mud banks in various positions just within its mouth. Evidently there is something in these situations, otherwise favourable, which prevents establishment; but whether the determining factor is scour or the higher salinity of the water, there exist at present no data to decide.

Colonisation by *Spartina* seems to follow the same general method of procedure in all cases. Single plants, dotted about, make their appearance as little tufts arising from seed. These rapidly expand through the agency of creeping stolons in the mud—a matter of some feet per annum—the tips of the stolons bending upwards to form the haulms of the grass, which in their turn tiller at the base. Roots of two kinds are freely produced; long, unbranched descending roots penetrating the mud to a depth of several feet (the extreme length found by me being 4 ft.) and serving for anchorage; and secondly, tufted, branched roots at the surface level, concerned especially with nutrition (Fig. 8).

Taking an area of 1 sq. decimetre (100 sq. centimetres) from a typically meadowed *Spartina* flat, the number of descending anchor-roots will be about 200 (2 per sq. cm. or 13 to the sq. inch). The green shoots of the current year rising from this patch will number about 24, whilst some 30 underground rhizomes should also be found, not counting numerous buds not in the elongating phase.

The *anchoring roots* arise from the base of the stocks where the green shoots are attached and also from the joints of the rhizomes. Whilst they are mainly unbranched, some, which are inserted rather higher up on the stock, carry lateral roots on the proximal 2 inches, whilst distally they descend, unbranched, into the soft, deep mud.

The *nutritive roots* form a dense plexus in the upper few inches of the mud. They are of limited extension, are inserted at a slightly higher level on the stools, and grow in various directions—vertically and obliquely upwards, horizontally and obliquely downwards. From the statement in the preceding paragraph it will be gathered that there are roots transitional between the extreme types; that a certain number of the anchoring roots perform in addition a nutritive function to a limited extent.

The clumps of *Spartina*, as they expand, commonly show a well-marked "marginal effect," i.e. the peripheral haulms exceed considerably in height those more centrally placed, so that the patch has a saucer-shaped appearance.

With further extension and massing of the units the same effect is seen at the margin of the area converted into "*Spartina*-meadow." The usual height of full-grown plants is 2-3 ft., varying according to season and location. Older, crowded plants reach the lower of these heights.

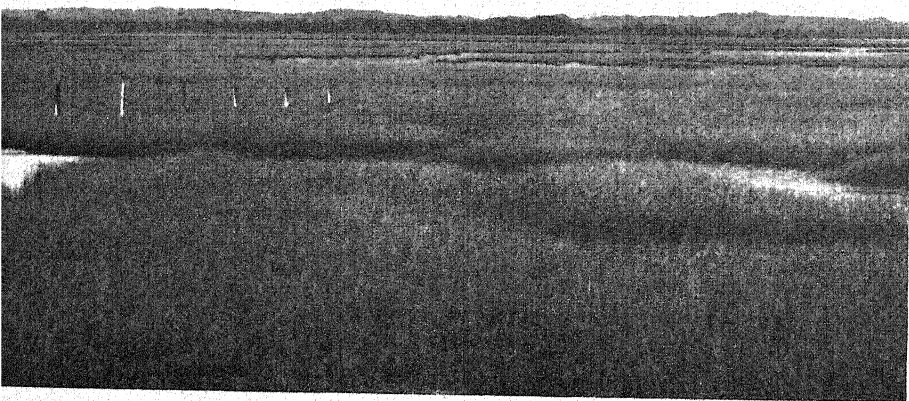
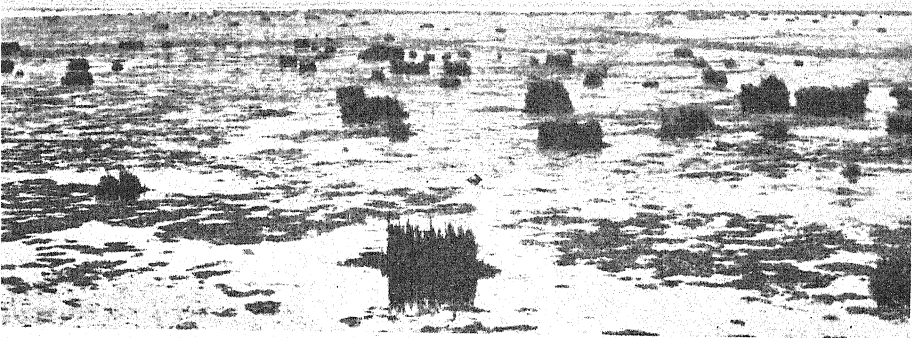
Colonisation is accompanied by a rise in ground level, due to silting. The permanent system of the plant holds mud and humus, the level is raised and the mud consolidated. In the Southampton and Poole Harbour areas it is not possible to stand on ground being colonised, and mud boards must be employed. Where "meadowing" has occurred the ground can be walked upon without special precautions.

To illustrate how quickly meadowing takes place two photographs of the same landscape taken from the same spot are reproduced here (Figs. 2 and 3). The view is Holes Bay, Poole Harbour, looking across from the west side in a north-east direction. The earlier photograph (Fig. 2), showing the early phase of colonisation, was taken in June, 1911, by Mr R. V. Sherring. The patches are about 2 ft. across. The second view (Fig. 3) was taken by me in June, 1924. In the interval of 13 years the small scattered patches have spread and fused into an all but continuous meadow. The distance of the railway at the back of the picture is between  $\frac{3}{4}$  and  $\frac{7}{8}$  of a mile from the camera.

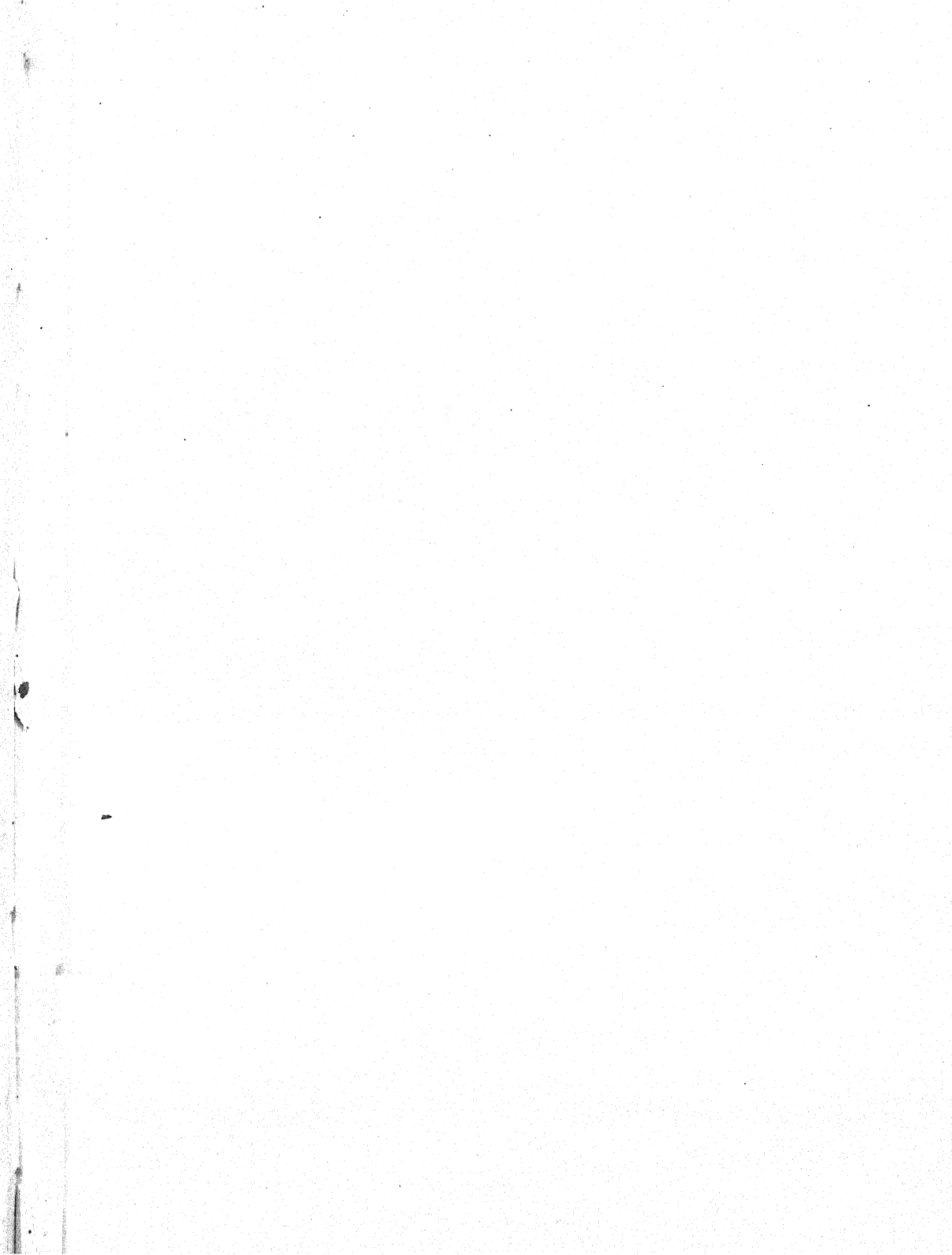
Others of Mr Sherring's photographs taken in 1911 stand in precisely the same relation to the present-day distribution as the one reproduced. Another of Mr Sherring's series, which was used as the frontispiece to Carey and Oliver's *Tidal Lands* (1918), shows the same order of *Spartina*-density as Fig. 2 above; at the present time the muds are here carpeted by an unbroken sward of *Spartina*, as seen from the original view-point.

A further illustration of the same thing is given in Fig. 4, taken from the French side of the Channel. In 1906 the French botanist Corbière reported finding a few scattered tufts of *Spartina Townsendii* in the Baie des Veys ("quelques touffes espacées, peu nombreuses"), the estuary of the rivers Taute and Vire, near Carentan, in the angle between the Cherbourg peninsula and the north coast of Normandy. In 1923, visiting the locality, I found what would be some 4 sq. miles of this estuary densely packed with the plant. The photograph (looking north) was taken from the sea wall  $1\frac{1}{2}$  miles west of the village of St Clément, on the east side of the estuary. The expanse of *Spartina* greatly exceeds any single stretch in Poole Harbour or the Solent, and is probably the most striking landscape of the kind in existence. The spread from a few scattered tufts to the present condition, which fills the horizon, is the work of 17 years.

A characteristic feature in the manner of extension over an invaded area must be described here. After the first invasion and establishment of small scattered *Spartina* units, the further spread is by no means equal everywhere. Whilst the original units appear to be distributed at random over the flats



FIGS. 2 and 3 represent the same view looking across Holes Bay, Poole Harbour, from the west side in the direction of the railway between Poole and Hamworthy Junction. They show the progress of colonisation by *S. Townsendii* between June, 1911, when the photograph reproduced in Fig. 2 was taken by Mr. D. V. Shaw, and 1913, when the photograph reproduced in Fig. 3 was taken by Mr. D. V. Shaw.





Aerial photograph of Brands Bay, Poole Harbour, taken by the R.A.F. and published by courtesy of the Air Ministry. On the left is Goathorn Point, with light railway line and jetty. Goathorn Point up to 1917 carried continuous woodland of *Pinus sylvestris*, of which now only non-serviceable residues remain. Brands Bay shows its system of creeks dividing the muds into compartments. The compartments are being colonised by *Spartina Townsendii*, which is in the phase of peripheral encroachment. At the top of the picture Fursey Island is seen, and on the right a portion of Studland Heath. The width of the picture is about 1 mile. Photograph taken June, 1924. From the point marked A on the plate the photograph, Fig. 5, was taken.

between the various creeks, the further peopling of the area is carried out (certainly in many cases) according to a perfectly definite scheme.

An arm of such an estuary as Poole Harbour is fed by a main channel, which, passing landward, divides repeatedly into lesser creeks, the ultimate ramifications of which interconnect like the capillary veins of a foliage leaf. In this way the muds are divided into areolae or compartments, separated by creeks. From the nature of the case some of these compartments will be entirely bounded by creeks, whilst others will be bounded in part by creeks, in part by the shore. When *Spartina* begins to mass the massing does not take place uniformly within the compartments, but peripherally along the margins. So that at a certain stage the compartments are presented as irregular figures with sinuous outlines, with the principal density of *Spartina* at the edge. The interior parts are still relatively open, but as time goes on these become gradually filled in until the only open water remaining consists of the creeks and "lakes"—areas where the depth is too great for *Spartina* to settle. The phase prior to complete meadowing is shown in Fig. 5, taken from the point marked *A* in Pl. I.

The regions where massing or meadowing is most rapid are the edges of the compartments which abut on the shore and the angles which lie in the forks of the branching creeks. Subsequently the rest of the perimeter thickens up, and last of all the interior parts of these hollow figures.

The process is illustrated by an air photograph (Pl. I) of Brands Bay, an arm of Poole Harbour lying between Goathorn Point and Studland Heath. The compartments, seven or eight in number, range from 15 to 30 acres each. In no case is massing complete, the central areas of the compartments being still relatively open. In time they should fill completely; the actual creek channels alone remaining free of *Spartina*. Inspection of the photograph (Pl. I) will show the features described—especially well in the lower part of the print. The width of the peripheral zone, though variable, reaches as much as 150 ft., whilst on the shore line it is considerably wider in the phase here shown (the point marked *A*).

Peripheral massing has been noticed in the case of other plants of the salt marsh. Annual forms of *Salicornia* at certain stages of the succession show a tendency to spread along creek sides; so too does *Aster Tripolium*. On many salt marshes *Obione portulacoides* is limited in its distribution to the edges of the creeks—its invasion of the compartments coming at a later stage, if at all. To such an extent is *Obione* tied to the bank that one almost looks for some special reason to account for its straying into the interior of the salting.

A case of this kind may be illustrated by an oblique aerial photograph showing in the foreground the Watch House marsh at Blakeney Point (Fig. 6). The darker, irregular figures which form the centres of the marsh compartments consist of a carpet of mixed halophytes, whilst the lighter marginal zones consist of a pure growth of *Obione*, which ultimately invades and

anchored and where consequently more seeds will be available. The outer members of the young community would seem to act as a partial physical barrier tending to trap and anchor drift (and seeds); the mechanism of dispersal thus discriminates in favour of the periphery of a compartment in contradistinction to its interior parts.

As to the zone of *Spartina* which establishes itself along the shore line, this is accounted for by the fact that sooner or later all drift not finding anchorage elsewhere will inevitably find its way to the shore. Actually, drift lines may occur on the shore even at a higher level than that at which *Spartina* will permanently establish itself. These are brought by high spring tides which submerge the *Spartina* zone, and if charged with seed this will germinate under the mulch of other drifted material and thousands of seedlings may arise though not one ultimately survive. Thus we see that tidal currents are no less inconstant and capricious agents for the conveyance of seed to the proper destination than, in other places, are the agencies of wind and animals. To meet such wastage and vicissitude plants in general produce seed on a lavish scale and the race can afford to lose the most of it without a set back.

The case of *Obione* seems different and the cause more obscure. *Obione* has a natural affinity for the banks of creeks. Something in the situation must favour it—mobility, aeration or access of drift. It is more than a mere expression of restricted seed dispersal, for in that case, sooner or later, the interior of the compartments would be invaded, and in the majority of cases they are not. In the case of the locality illustrated (Fig. 6) the *Obione* is finding its way slowly into the central areas, a stage reached in several of the older marshes of the Blakeney Marams.

Where there are extensive, level mud flats, as in the case described in the foregoing, *Spartina* tends to establish itself by peripheral invasion of compartments. Often, however, the ground slopes up gradually from the channels to the shore without any development of flats. In this case the plant will occupy a marginal region, a belt parallel to the shore and not extending down more than 2-3 ft. below high-water mark. If there is present already a marginal strip of ordinary salt-marsh, the *Spartina* establishes itself outside this, as at Sallenelles, near the mouth of the Orne in Normandy (Fig. 7), but subject of course to the vertical limitations aforesaid. In addition to occupying the bare muds, it tends to spread into the salting, often getting a dominant hold in a few years and ultimately replacing the ordinary halophytes usual in such situations. On the whole, successful invasion of these marginal strips (which carried a salt-marsh vegetation prior to the appearance of *Spartina*) is more frequently shown in the French localities than in the English.

But when *Spartina* strays too high it does not find such easy conquests. Thus, at the head of Brands Bay, Poole Harbour, it has invaded an extensive zone of *Juncus Gerardi*, and when last seen there was no reason to suppose that the *Juncus* would be replaced by the *Spartina*. Nor have I ever seen



*Phragmites communis* giving place to *Spartina*. With another of the larger halophytes, *Scirpus maritimus*, the result seems to be different. When *Spartina*, in close formation, comes alongside a belt of this plant it finds a way of growing through and overwhelms it in detail. Examples of this are to be found in Poole Harbour.

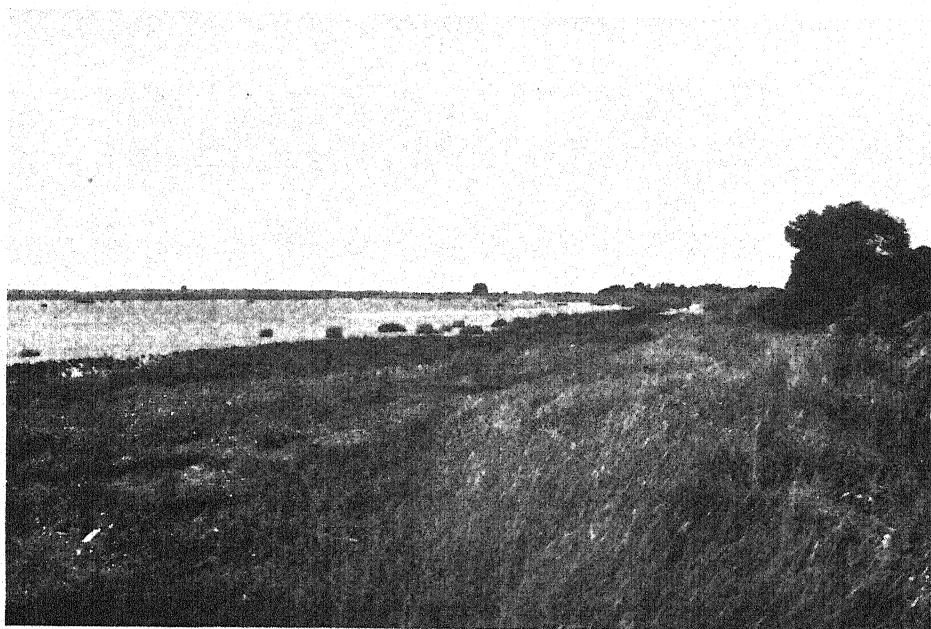


FIG. 7 represents an early phase of colonisation at the mouth of the Orne,  $1\frac{1}{2}$  miles north of Sallenelles. *Spartina* is establishing itself in tussocks on the mud just outside a strip of saltings. In the distance colonisation is reaching some density. First record in this locality, 1918. Photograph taken September, 1923.

#### THE USES OF *SPARTINA*.

When a plant appears and spreads miraculously, so that it occupies thousands of acres in pure stands, and is continually invading fresh localities, the question of economic application is sure to arise.

As a fodder, *Spartina* is eagerly devoured by beasts of all kinds. I have seen cows, horses, ponies, donkeys, pigs and sheep grazing on it in Poole Harbour. They go down to the meadows almost before the tide has run off and gorge themselves on it. Farmers find *Spartina* to be a useful reserve feed, and it is cut and stacked for winter use. Opinions differ as to whether it taints the milk or not, but on the whole the weight of opinion seems against using it for dairy cows. So far as I know proper feeding tests have never been made.

As to its suitability as a raw material for the manufacture of paper, experiments were made during the war. Though suitable in several respects, the



resistance of the fibre to bleaching prevents its adoption for fine papers. Though doubtless suitable for brown paper or boards, the price obtainable for a low-grade product of this kind would not cover the cost of harvesting, drying and transporting a crop like *Spartina*. If this plant is to find a place in paper exploitation, it must be as a raw material for high-grade papers (cf. 18).

Other uses for *Spartina* are sure to present themselves as knowledge increases of the ways in which plants may be chemically exploited for particular purposes. The important points in the present case are the extent, purity and density of the stands, combined with relative ease of harvesting.

At the present time the most obvious economic application of *Spartina* is to use it for the reclamation and stabilising of muddy foreshores. There is no plant in the world better fitted for this particular purpose, provided it be placed in positions comparable to those which it naturally occupies. *Spartina* has the conspicuous and unique faculty of colonising soft, "bottomless" muds which have resisted for ages the entry and establishment of other halophytes. With these it is not a matter of unsuccessful competition with other plants, but sheer inability to cope with the physical characteristics of the habitat. The ground I refer to is soft, viscous mud, most impermeable to penetration by oxygen, and from its viscosity affording an indifferent anchorage. That they may establish themselves in such places, plants require to penetrate the medium in all directions and to carry their anchoring roots rapidly to depths not necessary in the case of firmer soils. At the same time there must be means of access for oxygen to the remotest organs of the plant in these non-aerated soils. In the case of *Spartina* this need is met by an ample provision of lacunae reaching from end to end of the plant (29), whilst, at the same time, the vigorous constitution of this plant ensures the rapid establishment of a hemisphere of deep penetrating roots.

Turning now to the yield of seed. My own experience, extending to several seasons, is that it is adequate and often abundant. At the same time *Spartina* has the reputation of being a "shy seeder" (26 and 27). Doubtless bad seeding years occur with *Spartina*, as with other plants, but I am disposed to think that the suddenness with which the grain disappears from the spikes when ripe and its transport to some remote drift line, has given the impression that less seed is produced than in point of fact is actually the case. In other words, the long period of seed ripening, the uncertainty of the time of ripening and the comparative inaccessibility of the plant, tend collectively to exaggerate the impression that the plant is a shy seeder. In the current year (1924), characterised by much rainfall, deficient sunshine and prolonged open weather in October–November, there is no shortage of seed. Ripening has been retarded and the number of abortive spikes is considerable, but ample seed is available.

The seed once detached from the spike finds its way to rather localised drift lines that require searching for. The seed, which ripens in various

exposures from the end of October well into December, germinates at once in the drift lines, where it lies covered by a mulch. Here in November sprouting grains are to be found in thousands, and they may be found sometimes germinating *in situ* (viviparously) in spikes still attached to the plant. It may be noted that the embryo is green at ripening, due to the presence of chlorophyll in the scutellum and elsewhere; this, although of no special use to seeds germinating in the obscurity of deep banks of tidal drift, must have a significance where isolated seeds become anchored to the mud by wefts of filamentous algae.

Seeds not only germinate speedily, but the percentage germination is high. Growing in their native mud, the young plants will be 6 or 8 inches high by the first summer; they carry at the base as many as 10 or 12 sprouting buds, including one or more stolons which will carry their buds to a distance. These are especially characteristic of established plants (Fig. 8). A dense tuft of roots is shown by yearling plants, both anchoring and surface—the former already reaching to a depth of a foot. By the second year the plant forms a typical tussock, 6–12 inches in diameter, and extends vegetatively in all directions.

Next to rapid germination, anchoring and spread, *Spartina* qualifies as an agent of reclamation by its capacity to arrest silt and so raise the general level. At the same time ground well penetrated by the plant becomes increasingly firm and can be walked on, where previously it was a viscous slough to be traversed only on mud boards.

For the purpose of establishing *Spartina* on new ground the usual practice has been to use offsets. This means laborious operations at both ends, as well as bulky transport and liability to deterioration *en route*. The advantages claimed are that establishment can be effected at any time, and that the plant at once gets a good hold of the mobile ground. My own impression is that seed is the proper means to employ. The technique involved is of the simplest. It should be scattered thinly on the mud where it is to grow, and not pressed into the ground. A covering of the natural drift of the locality (e.g. algae such as *Rhizoclonium* or filamentous *Enteromorpha*, leaves of *Zostera*, etc.) should be spread over it and this pegged down to keep it in place till germination has secured the young plants in the habitat. Placed lower than the natural zone, establishment fails, alike by seed or offsets.

In nature distribution by seed is supplemented by offsets, but it is to be questioned if this method accounts for more than a small fraction of the total propagation.

Established plants are liable to be scoured out in the following way, and such detached specimens, drifting and becoming arrested somewhere, may take root. In Poole Harbour, and doubtless elsewhere, *Spartina* settlements in exposed positions, especially when the level has been raised above the surrounding muds through silting, become liable to wave erosion. In this way



FIG. 8. *Spartina Townsendii*; simplified sketch of base of plant to show the relations of under- and above-ground organs. The aerial shoots arise from a plexus of rhizomes occupying the zone below the surface. On the bases of these shoots and on the rhizomes are produced (1) quantities of surface roots clothed with lateral roots, (2) straight, unbranched, descending, anchoring roots, which penetrate the mud to a depth of several feet. Such of these anchoring roots as arise relatively high up carry laterals where they traverse the surface layer. Scale: about one-third nat. size.

the edge of the settlement, on the exposed side, is subject to undercutting and the mud is washed away from the roots. The resulting disrooted fringe of *Spartina* is tossed this way and that by the restless elements, and, separating into fragments, is drifted away.

Latterly, this erosion of *Spartina*-fields has assumed a considerable importance in the more central parts of Poole Harbour. From this point of view there are two sorts of localities where *Spartina* spreads. There are, on the one hand, the bays and bights of the harbour which are practically unaffected, and there are the shallow muds which project into the open harbour from the points of land between the bays. On these latter positions extensive *Spartina* meadows have developed, and these, as they increase in height, are especially liable to erosion. Where the "slog" of the waves strikes such a *Spartina*-field, more or less at right angles to its length, it will be cut back, and at places actually penetrated. Once this has happened the process of destruction is rapid and the whole area may be swept away.

The ground thus eroded is left bare; for the *Spartina* has gone, and the *Zostera* which preceded it had been previously obliterated by the *Spartina*. There is no sign of recolonisation of such areas by *Spartina*, and it remains to be seen whether the *Zostera* will come back. Typical affected areas are to be found in Poole Harbour to the north and south of the Wych Channel in the neighbourhood of Shipstal Point. Already some scores of acres must have been eroded in this way and it is to be expected that more will be involved. Nevertheless the total area liable to effacement from this cause represents only a small percentage of the total area occupied, when the whole of Poole Harbour is considered.

Apart from cases like the above, and a single example of a few acres killed by a creosote effluent in Southampton Water, *Spartina* seems unchecked in its onward march. No evidence has yet accrued to indicate that *Spartina* is to be superseded by any other plant combination; such a succession is of the natural order of things, though it may take centuries to accomplish.

As regards the immediate effects of the *Spartina* invasion certain facts emerge relevant to the present discussion.

With the ebb and flow of the tide in a muddy estuary a large amount of silt is carried backwards and forwards. Where the upper muds are colonised by such a plant as *Spartina* much of the silt will be held by it and the level slowly rise. In other words, the mobile silt of the channels and waterways tends to be fixed at a higher level. The immediate consequence of this is a deepening and perhaps a widening of the channels—as is reported by fishermen at Poole. In process of time, when *Spartina* has occupied fully the available ground, the amount of mud that can be assimilated will reach its limit. For as the level rises the rate of silting will decrease till it becomes inappreciable. Concurrently with this rise of the *Spartina*-covered flats, there will be a corresponding exclusion of tidal water, and mobile mud will once more encumber

the channels. As there is less water, there will be less scour at the ebb to clear the channels; so that if navigation is a consideration, it will have to be maintained by dredging. And if, at this stage, the *Spartina*-fields being ripe for the operation, parts of the harbour are banked off and reclaimed, this will start the *Spartina* on a fresh period of colonisation with consequences of the same order, only intensified.

For it is usually to be observed on most salt marshes that the saltings reach out from the edge of the estuary a certain distance in the direction of the main channel, but advance no further. The muds beyond remain uncolonised; a state of equilibrium has been reached. This is attributed to the scour caused by the tidal water, as it ebbs from the saltings, preventing any permanent accumulation of silt beyond the limits reached. Directly the saltings are banked off and this scour diminished, fresh growth of marsh starts in front of the bank and the muds of the estuary are still further encroached on. This is how it is that silting up combined with reclamation operates to the disadvantage of navigation. It is the age-long antagonism between land and water, the interests of the landowners and of the shipping community. Now *Spartina* as an agent is not qualitatively different from other denizens of the foreshore; it is merely an astonishingly vigorous and pushful halophyte, capable of occupying ground usually left uncolonised by other halophytes.

In view of the foregoing it is evident that a considered judgment of the policy involved ought to precede any steps that would lead to results jeopardising navigation. Apart from such cases there must be many extensive coastal and estuarine areas marked out for reclamation, and it is especially in such cases that the suitability of a course of *Spartina* might be considered. The antecedents of ground to be enclosed must have a bearing on the qualities of the soil in the reclamation, and as knowledge of the properties of the various halophytes and their relation to the silting process increases, this, the agricultural or farming aspect of reclamation, should become at least as important as the engineering. In this connection it may be remarked that recently Holland has begun to show an interest in *Spartina* in case the plant might prove of value in the reclaiming and polderising operations for which the Dutch are world famous. The matter is mentioned here for the encouragement of others in a position to cultivate and watch the progress of this plant. Information is required especially in connection with its adaptability to different maritime soils, exposures and ranges of temperature. Small experiments, it is true, are being made here and there in this country, but *Spartina* would appear to possess wider usefulness and to merit fuller trials than any hitherto devised.

THE STATUS OF *SPARTINA TOWNSENDII*.

Curiously enough, in spite of the attention which this plant has attracted, the status of *S. Townsendii* still remains unsettled. Discovered at Southampton in 1870 it was recorded as a variety of *S. stricta* (Groves, 8), later described and figured as a distinct species (Groves, 9). Stapf in 1908, being unable to match *Townsendii* with any of the American forms, concluded that it was distinct. To account for it he put forward the hypothesis that it was a naturally produced hybrid of *stricta* and *alterniflora*; this was based partly on botanical grounds, partly on the occurrence near Bayonne of *S. Neyrautii*, which is in effect the counterpart of *Townsendii*, both in respect of its characters and of the circumstances of its occurrence (Foucaud, 1895). This view based, as Stapf tells us, largely on circumstantial evidence (Stapf, 27, p. 80) has held the field.

Latterly, the interest aroused by the remarkable spread of *S. Townsendii* on the north coast of France has led to a further consideration of the matter. Corbière and Chevalier (6), who had studied the plant in its French localities, argue that *S. Townsendii* cannot be a hybrid because it seeds abundantly, has normal pollen, and because one of the alleged parents (*S. alterniflora*) does not occur in the north of France. They conjecture it to be identical with the American *S. glabra* var. *pilosa* and suppose it to have been introduced directly from the U.S.A. So far as this last point is concerned, having regard to the identity of *S. Townsendii* on either side of the Channel, it seems more probable that the plant found its way from England by seed distributed by shipping—especially as the first record for the north of France is 1906, a date when *S. Townsendii* was spreading everywhere in the waters around Southampton.

The first point to be certain about is whether *S. Townsendii* is really a distinct form. Stapf has gone very fully into this matter (26), and there seems no reason to doubt his conclusion that it does not match any of the related North American varieties. These include *S. alterniflora*, *S. glabra* and *S. pilosa*, all regarded as varietal forms of the *alterniflora* group. Whether they are varieties or species, seems immaterial. To these is to be added *Townsendii*, which, like *pilosa*, has the pubescent upper empty glume, but has more slender spikes, and the spikelets less densely arranged on the spike than *pilosa*.

If then *Townsendii* be accepted as distinct, it must have arisen from another form or forms, either in European or American waters. As it has not been recorded for America, the latter alternative need not be considered seriously.

*Townsendii* therefore appeared at Southampton, and later (where it was called *Neyrautii*) near Bayonne. It may be a sport or mutant of *alterniflora*, or, on the other hand, a hybrid between this species and *stricta*.

If it is a hybrid, then it should betray its hybrid constitution. In one

respect it does this, viz. in the extreme vegetative vigour which it displays. A vigorous constitution of this kind is not unusual in a first cross; what is surprising is that not only is this vigour maintained through many seed generations but that the plant should remain substantially uniform. There is no indication of segregation, which is certainly to be expected in an ordinary hybrid. This circumstance, which at first sight seems to negative the hybrid theory, does not however absolutely close the door to it, because there exists a class of hybrids characterised by perfect stability. But it would be premature to assert that *S. Townsendii* belonged to this class, without the production of evidence. This can be obtained only by breeding experiments and cytological investigations carried out on the relevant forms, which would have to be cultivated under controlled conditions. Whilst such an investigation is in progress it would be desirable that the various related forms of *Spartina* that have been brought into the discussion should also be assembled and grown side by side. In this way the whole matter could be thoroughly thrashed out. The problem is somewhat complicated because the forms involved are mainly American, whilst the theatre of active interest, in which the *Spartina*-equilibrium has become unstable, is European. Certainly the present tripartite discussion across the Atlantic and the English Channel is an inconvenient method of settling anything and is hardly likely to lead to any definite result.

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# MARINE PHYTOPLANKTON OF THE WELSH COASTS, WITH SPECIAL REFERENCE TO THE VICINITY OF ABERYSTWYTH

By BLODWEN LLOYD.

(With five Figures in the Text.)

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## I. INTRODUCTORY.

IN the course of work done on the marine phytoplankton of the Welsh coasts, attention was paid more especially to the area in the vicinity of Aberystwyth. For purposes of comparison, visits were also made to, and samples obtained from, other parts of the Welsh coasts. As the work done was carried on from a land station, it was found that a study of the free-floating plant organisms as such tended to include also those forms which are not, strictly speaking, planktonic, but which occur as regular components of the plankton flora wherever coastal influences are in evidence. As compared with the open ocean, the distinguishing feature of such offshore or neritic areas is the considerably greater variation in hydrographic conditions, this in turn making for a correspondingly wider range of variation in the plankton organisms themselves.

For such a specialised coastal community various terms have been proposed; Haeckel names it the "meroplankton" as distinct from the "holoplanktonic" or "holopelagic" ecological unit of the open sea<sup>1</sup>. Schimper's term "hemiplankton" connotes much the same plankton-association of the coast-line. Kolkwitz<sup>2</sup> advocates the use of the term "seston," but, including

<sup>1</sup> Schimper, A. *Plant Geography*. Oxford, 1903.

<sup>2</sup> Kolkwitz. "Plankton and Seston." This JOURNAL, 1913.

as it does the whole of the material occurring as free-floating or suspended particles in the water, it has the disadvantage of embracing not only sporadic non-planktonic living forms, but also much extraneous material such as dead leaves.

The work done consisted primarily of a detailed investigation into the nature of the phytoplankton of the area, with special reference to temporal and spatial variations, and to conditions affecting the same. As far as possible, ecological units of association were evaluated, and features of special biologic interest in the plankton forms themselves were correlated with functional adaptations. The resulting data were compared with other plankton records for various districts, and also with earlier figures for this place. Previous records for Welsh waters are those of Gough and Bygrave<sup>1</sup>, who give a frequency-table for plankton throughout 1905, from tow-nettings from the lightship stationed in Cardigan Bay at that time. Further, the Welsh coasts, being under the jurisdiction of the Lancashire and Western Sea Fisheries Board<sup>2</sup>, were visited, usually four times a year, by their boat the "John Fell" and its successor, the "James Fletcher." The results are given in their yearly reports, which give frequency data, among other places, for Red Wharf Bay, off Anglesey, and Carnarvon Bay, together with some discontinuous records for Cardigan Bay.

For "regular" sampling the nets were towed along a given course for 15 minutes from a small rowing boat<sup>3</sup>. As far as conditions of tide and wind permitted, the hauls were made along the same course each time, some  $1\frac{1}{2}$  to 2 miles from shore (Fig. 1). This course extended somewhat obliquely across the bay, in the outer waters beyond the inshore waters. Tow-nettings against the tidal stream were found to give a bigger haul; accordingly, at ebb tide the haul was made from the southern end, and at flow tide in the opposite direction. In either case, a tow-netting was also made back along the course. With the tides prevalent here, there was usually a marked difference in the rate of the boat's movement under the two sets of conditions. It was ascertained that a slackening of speed resulted in the nets fishing in lower waters, and so catches were thus made both from the surface and from the sub-surface layers.

In addition to these "regular" samples, catches were also obtained from farther afield.

## II. NATURE OF AREA STUDIED

In addition to the detailed work done on the phytoplankton of Aberystwyth, samples were obtained at different times from the following places: Red Wharf Bay, off the north-east coast of Anglesey; Moelfre, off the south-west coast of Anglesey; Bangor, on the Menai Straits; Saundersfoot, off the south

<sup>1</sup> Gough and Bygrave. *Report on the Plankton of the English Channel, International Plankton Investigations* (Marine Biological Association). 1906.

<sup>2</sup> *Yearly Reports, Lancashire and Western Sea Fisheries Board, 1904 et seq.*

<sup>3</sup> The details of the technique employed will be fully described in a forthcoming paper.

coast of Pembrokeshire; and also Port Erin, Isle of Man. Any special features of these places will be considered as occasion arises, but as the greater part of the work done centred round the Aberystwyth waters, the nature of this district will be considered here.

Geologically, Cardigan Bay comprises three drowned valleys running N.N.E. and S.S.W., parallel with the still terrestrial promontories of Carnarvonshire and Pembrokeshire. The corresponding drowned ridges remain vestigially as three "Sarns"—Sarn Badrig off Harlech, Sarn-y-bwch off Towyn and Sarn Cynfelin off Aberystwyth. These constitute shoals of some danger, and have a considerable effect on local currents. For instance, the proximity of Sarn Cynfelin gives rise to certain local peculiarities south of Aberystwyth, the tidal streams run N. parallel to the coast at no great speed, 1 knot at spring and  $\frac{1}{2}$  knot at neap tides, as far as Cynfelin Patches (Fig. 1). "Here the stream meets a line of shallow water extending across their path a distance of 5 miles from the shore, and this diverts the north-going stream in an easterly direction south of Cynfelin Patches, though outside the west end of these patches the streams run in a northerly and southerly direction. Both streams have an indraught towards the shore<sup>1</sup>." This inshore deflection causes a swifter south-going current (coastal) to flow past Aberystwyth independently and two hours before the ebb tide of the offshore waters.

An important hydrographic feature is the absence of great depths, the 25 fathom line being well outside Cardigan Bay. Just off Aberystwyth there is no greater depth than about 7 fathoms, but some 4 miles southward along the coast are the trawling grounds down to 14 fathoms deep; this deep runs parallel to the coast, and is known locally as "the Gutter" (Fig. 1).

Aberystwyth lies in the concavity of Cardigan Bay, and, owing both to the shallowness of its harbour and the proximity of the Cynfelin shoals, is too inconvenient a port of call. In fact, except for the local trawlers, there are only pleasure motor-boats in the summer, and occasional boats freighted with grain or cement, so that this stretch of coast-line is remarkably free from industrial contamination.

The general trend of climatic disturbances is in a direction roughly parallel to that of the structural lines. Cardigan Bay itself offers a fairly open path to Atlantic areas of barometric depression, and it catches much of their force as they travel across, usually in a N.N.W. direction; high winds and rough seas are therefore extremely frequent here in the winter months. However, this same accessibility of Cardigan Bay would tend to admit any ameliorating southern influences, as for example the streaming of the postulated warmer offshoots of the Gulf Stream around the north European coasts. But in addition to the incoming of southern waters, the evidence from drift-bottles<sup>2</sup> seems to show that there are also south-going currents into Cardigan Bay

<sup>1</sup> "Tidal Streams of the West Coast of England." *Admiralty Report*, 1901.

<sup>2</sup> J. Johnstone. *Report of the Lancashire Sea Fisheries Laboratory*, 1902.

from the Irish Sea. The latter is allied hydrographically to the northern neritic waters off Greenland and Iceland; hence Cardigan Bay might reasonably be presupposed to show some traces of both northern neritic and temperate Atlantic influences. How far the plankton of this district is affected by either will be considered later.

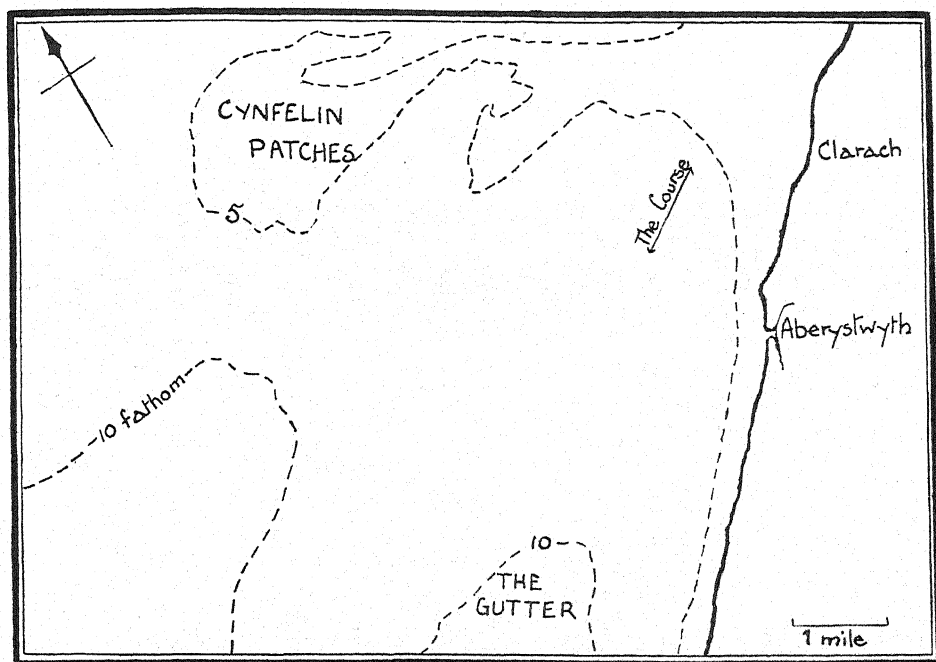


FIG. 1. The waters off Aberystwyth.

### III. HORIZONTAL DISTRIBUTION.

As stated previously, the further we advance from the coast-line, the more uniform do hydrographic conditions become, until we arrive at such an extreme as the "halistatic" areas of the oceans, notably the Sargasso Sea. Schimper states that plankton is typically developed only above very deep water; hence his use of the term "hemiplankton" for the free-floating flora of coastal waters. Schutt, on the other hand, holds that those oceanic areas far removed from land are, so to speak, deserts, at least as far as the development of plankton is concerned. Of all aquatic communities, that of marine coastal areas is the most cosmopolitan, including as it does not only characteristic neritic, but also oceanic forms carried coastwards by currents, brackish-water and even freshwater forms swept down from the estuaries, epiphytes detached by wave action, and, lastly, benthon whirled up from the sandy substratum.

In considering the hemiplankton, as in the flora of any given area, there is a three-dimensional variation to be considered, namely, of latitude or horizontal distribution, of altitude or distribution in depth, and of time. In referring to the area under consideration, horizontal differentiation resolves itself mainly into a question of the degree of proximity to the coast. The most distant tow-nettings were made some 8 to 10 miles from the shore, but a fairly well-marked difference in the nature of the hauls was observed at a considerably less distance. I take the further tide-line as the line of demarcation between neritic phytoplankton proper and the flora of the inner waters. After heavy rains this can be seen very distinctly, the inshore waters being a murky yellow with suspended fluvial material, as contrasted with the green or blue of the outer sea. Even on calm days it is distinguishable as a line of flotsam, or sometimes by a difference in the appearance of the surface waters. This line naturally varies in distance from shore with the state of the tide, but is roughly 1 mile off the shore; it is from the purer, more homogeneous outer waters that the "regular" tow-nettings were taken. Thus we have (1) the type-zone, or *neritic* zone proper (see Sections IV and V), and, nearer to land, are the variations from the flora of this type-zone, namely (2) *littoral intertidal* and (3) *brackish water*.

Within zone (2) I have included not only that area which may be left uncovered by spring tides, but also as far out as the above-mentioned tide-line; this marks the reasonable offshore limits of tidal influences and of the coast-line itself. As contrasted with the neritic zone, the littoral intertidal area shows greater variation in salinity, greater susceptibility to tidal influences and surfs, and a consequently higher admixture of other than plankton organisms. This generalisation applies to the whole of the coast-line, but at any given part there may be originated special local peculiarities.

Within a limited area along this coast, i.e. from South Shore to the north of Clarach Bay, three distinct edaphic shore-types occur (Fig. 2). A study of the inter-relationship of these with the proportionate occurrence of phytoplankton, motile and sessile benthon was made. The special development in rock pools will be dealt with separately.

The following types of shore-line were found to give rise in their immediate vicinity to a free-floating flora of special associations:

- (i) Coarse sandy bay, as in the main bay, or at Clarach.
- (ii) Shale reef, as below the College.
- (iii) Coarse shingle, as at South Shore.

In addition to the planktonic, usually non-motile forms, there also occurred in these shore waters:

- (i) Normally epiphytic forms which had become detached by surf action. Such forms might continue life with free-floating habit; and *Grammatophora marina* was found to develop under such conditions a secondary film of mucilage.

(ii) Motile benthic forms whirled up from the substratum by currents and wave action often become temporary components of the hemiplankton.

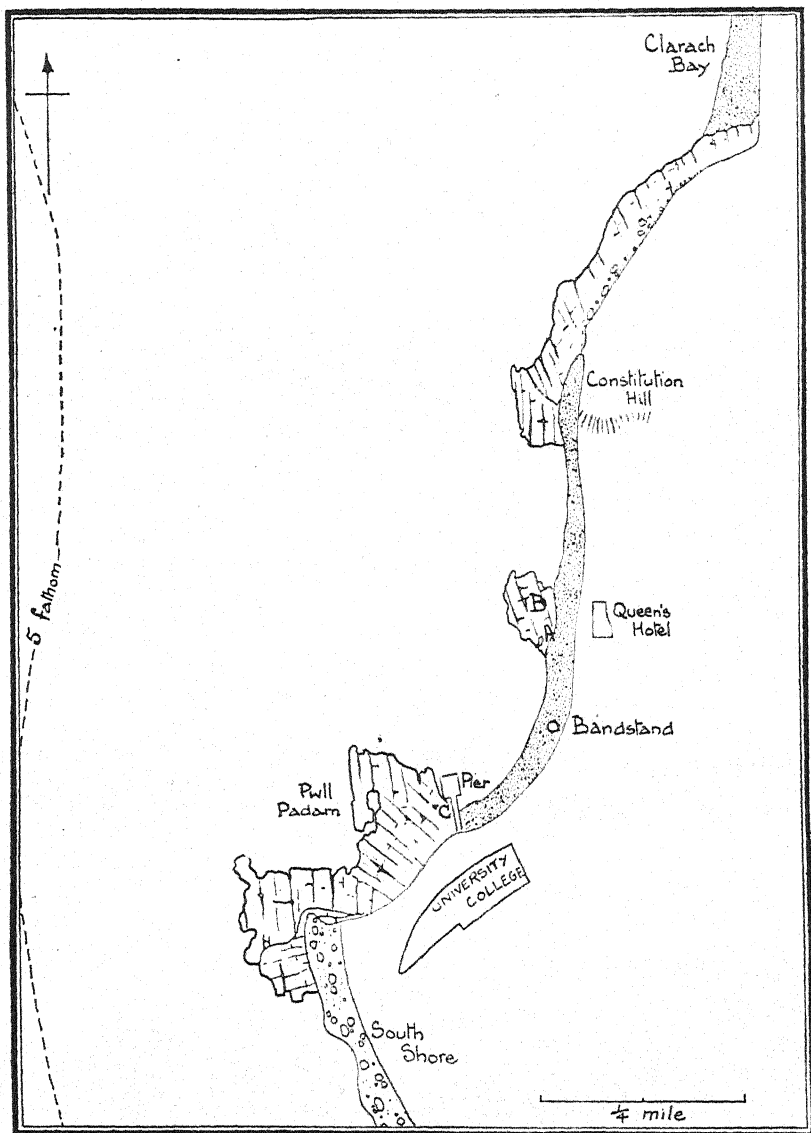


FIG. 2. The shore line at Aberystwyth.

It was found impracticable to use the tow-net for the capture of free-floating organisms along the shore-line. Accordingly, the filtering method with the small conical net was adopted; the catch was then collected into formalin, allowed to settle, and the sediment transferred to a cavity slide for

estimation. Material obtained in this way from the shore-line was naturally mixed with much sand, small Ectocarpus and Ceramium; on such occasions the water-samples were first freed from these small algae and from polyzoa by filtering through coarse muslin. The end of the pier was found to be a very convenient station for such filtering work.

TABLE I. *The Microphytic Flora of the Shore-line Waters.*

	1. Sand		2. Reef		3. Shingle	
	Main Bay	Clarach	College	Queen's Hotel	Const. Hill	South Shore
<b>EPIFLORA</b>						
Achnanthes brevipes	—	—	f.	—	f.	f.
" longipes	c.	c.	c.	f.	f.	—
Synedra fulgens	f.	—	c.	f.	f.	—
" radians	—	—	f.	—	f.	—
Grammatophora marina	f.	f.	c.	c.	c.	—
" macilenta	—	f.	c.	f.	c.	—
Licmophora flabellata	—	—	f.	f.	—	—
Schizonema spp.	f.	c.	c.	c.	c.	f.
Rhabdonema arcuatum	—	—	—	—	—	—
<b>MOTILE BENTHON</b>						
Stauroneis salina	c.	c.	f.	f.	c.	—
Amphora marina	f.	c.	—	—	—	—
Pleurosigma attenuatum	c.	c.	f.	f.	—	—
Surirella gemma	f.	f.	—	—	—	f.
Achnanthes parvula	—	f.	—	—	—	f.
<b>PLANKTON</b>						
Actinopterychus undulatus	—	f.	—	—	f.	—
Biddulphia mobiliensis	—	—	f.	—	—	f.
Coscinodiscus radiatus	—	f.	—	—	f.	—
Chaetoceros curvisetum	f.	—	f.	—	—	f.
Melosira borrii	—	—	—	—	—	f.
Nitzschia closterium	f.	—	f.	—	—	f.
Streptotheca thamensis	c.	f.	f.	—	—	f.
Thalassiothrix nitzschoides	—	f.	—	—	—	f.

c. = common. f. = frequent.

A method employed previously was to take a litre of sea-water and fix any included organisms by the addition of 40 c.c. Flemming's solution; this was allowed to stand for several days in a tall measuring cylinder for the sedimentation of the contents. This usage probably entailed some loss of contained organisms, and was later replaced by the centrifugal method.

From observations made chiefly during October to December, 1922, a table was drawn up for certain localities exemplifying the different types of shore-line. The species found are given in Table I, and the forms found are recorded as c. (common), or f. (frequent). If this table be summarised, the following results are obtained:

	Sandy Bay		Shale Reef		Shingle	
	Main Bay	Clarach	College	Queen's Hotel	Const. Hill	South Shore
Epiphytes	1c. 3f.	2c. 3f.	6c. 3f.	2c. 7f.	3c. 6f.	2f.
Benthos	2c. 2f.	3c. 2f.	. 2f.	. 2f.	1c. .	. 1f.
Phytoplankton	1c. 2f.	. 3f.	. 4f.	. .	. 3f.	. 6f.

This shows clearly a predominance of a different type of ecological unit in each of the three kinds of shore-line. That is to say:

(i) Where the waves break on the shale reefs, epiphytic unicellular forms, diatoms chiefly, tend to become detached in large numbers, and to form no small proportion of the free-floating flora; such fortuitously planktonic forms may continue to reproduce and may even develop temporary retrograde characters. The increased mucilage of *Grammatophora* has already been noted, but in addition it was often found that the endochrome fragments into irregular plates and is of a lighter golden-brown colour (Fig. 3).

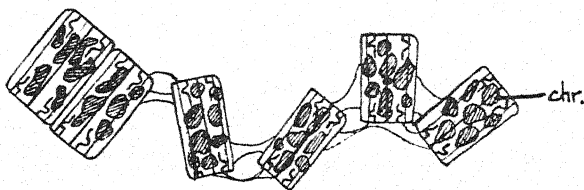


FIG. 3. *Grammatophora marina*, found free-floating.

(ii) Where there is a bottom of coarse sand, there are abundant creeping benthic forms, chiefly *Navicula*, *Pleurosigma* and *Nitzschia* spp. Many of these are tossed into the upper waters by the advancing tide, and so, especially in the surf-line, we have a great abundance of them.

(iii) Over shingle, the smoothworn shale and mudstone pebbles afford neither support for epiphytes nor substratum for creeping forms, hence the chances of these two types occurring are about equal. The surf waters of South Shore, therefore, were characterised by only occasionally present epiphytes and benthos; there was a predominance of the truly planktonic forms, but even these were scarce.

In connection with this branch of the work an interesting point observed was that collections made on calm days yielded more diatoms, especially plankton diatoms, than those of stormy days. Possibly this is due to the fact that it is the upper waters that break as waves, and that on calm (or sunny) days the microphytes will be concentrated in these upper layers; the breaking of the waves then tends to carry shoreward a greater number of organisms.

#### *Microphytes of rock pools.*

Rock pools, with their comparative calm, much greater insolation, and higher concentration of life forms, make for somewhat more specialised conditions of life. In the case of macrophytes, semitropical forms may be found in the rock pools of temperate regions; the free-floating forms, on the other hand, are disturbed twice daily at an interval of time varying with the state of the tide and with the horizon of the pool in question. Hence the rock pool cannot be said, strictly speaking, to have a free-floating flora peculiar to itself, except in so far as the ordinary microphytes of the shore-line are



confined therein for those few hours, or where organisms are generated during that time of exposure.

The microphytic flora of those pools selected for observation was collected largely by means of the filtering method, but sometimes also by centrifugal means. In order to ascertain any possible changes during the time when the pools were uncovered and hence undisturbed by the tide, three pools, A, B and C, were kept under observation (Sketch-map, Fig. 2). On one occasion, Pool B (Ascophyllum zone) was examined by filtering a litre of water at intervals of two hours; the following results were obtained; they are considered as typical:

(1) *Two hours before being covered*: numerous benthic forms, also *Schizonema Grevillei*, *Amphora complanata*, *Synedra radians*, *Rhizosolenia semispina*, *R. shrubsolei*, *Paralia sulcata*, *Grammatophora marina* and *Achnanthes longipes*.

(ii) *Immediately before*: as above.

(iii) *Immediately after*: the same, but in fewer numbers.

(iv) *Two hours after*: mixed shore flora. By gently lifting out the smaller branched algae, as *Ectocarpus*, and allowing them to drip into specimen tubes, much of the phytoplankton left by the receding tide and entangled in the branches, could by these means be collected.

(v) *Four hours after*: as in (i).

TABLE II. *The Microphytic Flora of Rock Pools.*

Phytoplankton	November 8			January 8			February 6			May 22		
	A	B	C	A	B	C	A	B	C	A	B	C
<i>Actinopterychus undulatus</i>	f.	f.	f.	—	—	—	—	—	—	—	—	f.
<i>Bacillaria paradoxa</i>	f.	—	—	—	—	f.	—	—	r.	r.	f.	f.
<i>Biddulphia mobiliensis</i>	—	f.	f.	—	—	—	r.	—	—	—	—	—
<i>Coscinodiscus radiatus</i>	c.	f.	f.	—	—	c.	f.	—	f.	—	—	—
<i>Chaetoceros contortum</i>	f.	—	—	—	—	—	—	—	—	—	—	—
<i>decipiens</i>	—	—	—	—	—	—	—	r.	—	r.	—	—
<i>Ditylium brightwelli</i>	—	—	—	—	—	—	—	r.	—	r.	—	—
<i>Oxyrrhis marina</i>	—	—	—	—	—	—	—	—	—	c.c.	c.c.	r.
<i>Paralia sulcata</i>	f.	—	—	—	—	—	—	—	—	—	—	f.
<i>Rhizosolenia semispina</i>	—	f.	—	—	—	—	—	—	—	—	—	—
<i>Streptotheca thamensis</i>	—	—	—	f.	f.	r.	—	—	—	—	—	—
<i>Thalassiothrix nitzschioides</i>	—	—	f.	—	—	r.	—	—	r.	—	—	—
<b>MOTILE BENTHON</b>												
<i>Druridgea geminata</i>	f.	—	—	r.	r.	f.	—	f.	f.	—	f.	f.
<i>Nitzschia</i> spp.	c.	—	—	f.	r.	—	—	f.	f.	—	—	c.c.
<i>Navicula</i> spp.	c.	f.	f.	—	—	f.	—	—	f.	—	—	—
<i>Pleurosigma</i> spp.	—	—	r.	—	—	—	—	—	—	—	—	—
<b>EPIFLORA</b>												
<i>Achnanthes longipes</i>	f.	—	—	r.	r.	f.	r.	—	—	—	—	—
<i>Amphora complanata</i>	r.	—	—	—	r.	—	—	r.	—	—	—	—
<i>Grammatophora marina</i>	—	f.	—	r.	r.	—	—	—	—	—	r.	—
<i>macilenta</i>	—	r.	—	—	r.	—	—	r.	—	—	—	—
<i>serpentina</i>	—	r.	—	r.	—	—	—	r.	—	—	—	r.
<i>Rhabdonema arcuatum</i>	f.	—	—	r.	r.	—	—	f.	—	—	—	r.
<i>Schizonema Grevillei</i>	—	f.	—	—	—	—	—	—	r.	r.	r.	—
<i>Synedra</i> spp.	r.	f.	r.	r.	c.	r.	—	c.	—	c.c.	r.	—

c. = common. f. = frequent. r. = rare.

Thus the associations presented for the shore-line proper has no analogy in the case of rock pools. Benthic forms were found to be fairly abundant, even in the smooth-sided rock pools empty of the larger vegetative forms; thus the rock pool microphytic flora may be considered to be in general of the same nature as that of the reefy shore-line. At all events, the results given in Table II seem to show that phytoplankton proper is not very abundant in rock pools; this is more probably due to the great mechanical wave stress to which it is subjected than to any unsuitability of conditions in the pools themselves. A curious fact in this connection is that those forms found to flourish in rock pools were those that succeeded best under artificial conditions, *Oxyrrhis marina* and *Nitzschia closterium* being the most striking examples. The former was found to occur abundantly in rock pools in the summer months, and seemed to reproduce with such extraordinary rapidity that even in the few hours of exposure, any one pool might swarm with *Oxyrrhis*. Thus we have here a normal phase of littoral species with also a few residual plankton forms left by the receding tide; and in the summer a special phase, with these forms in about the same number, but with swarms of minute usually motile protista.

Apparently we have in the rock pool a natural approximation to cultural conditions, and where the intertidal spaces of time allow, there is a tendency to the development in the summer months of a swarm-flora widely different from that of the open shore.

#### *Plankton of Brackish water Regions (Hyphalmyroplankton).*

Brackishwater regions are represented in this area by the mouths of the rivers Rheidol and Ystwyth with their backwaters, and, in the case of the river Dyfi some miles to the north, by a considerable extent of salt flats. The type area selected for study was that of the Aberystwyth harbour, at the mouth of the river Rheidol; here there were special features connected with the contamination of the river waters. Samples were also obtained from St Bride's Bay on the Severn estuary.

Brackishwater regions may be more or less self-contained, and shut off from outside influences, e.g. the salt pannes of the higher levels at Ynyslas, near the Dyfi estuary; or they may be subject to two sets of often opposing influences, as at the mouth of any river. On the one hand we have marine, and on the other fluvial conditions. For example, the tidal fluctuations of the former would tend to oppose in varying degree the unidirectional flow of water from the latter.

As compared with the open sea, the harbour shows a greater degree of variation about a much lower salinity; in April, 1923, the chlorine content of water samples off the end of the harbour jetty was only 2.5 parts per mille, as compared with 18 to 19 parts (34 to 36 total solids) in the open sea. On the contrary, the salt pannes of Ynyslas, with considerable evaporation but

no freshwater inlet, vary from 8 to 16 parts of Cl. (These figures were kindly given me by Mr W. M. Speight, M.Sc., Zoology Department.) The Aberystwyth harbour is further differentiated from the sea by the fact of its being sheltered from the prevailing S.W. winds.

As compared with the river proper, it shows greater salinity, subjection to tidal variations, and more terrestrial impurity in suspension. The area under consideration is protected to windward by a natural shingle bank which has been built up into a breakwater. The harbour is extremely shallow, and low tide uncovers a coarse shingle deposit (fluvial); but there is a central channel bottomed by dark mud, principally of shale fragments. This affords a substratum for creeping benthic forms. The chief macrophytes in the harbour are *Fucus ceranoides* and *Enteromorpha intestinalis*; these grow abundantly, but a diatom epiflora is scarcely common except on the tips of some *Enteromorpha* filaments.

Such a region, intermediate physically between the salt water of the sea and the fresh water of the river, would tend to contain plankton types characteristic of each of these areas, and possibly also some peculiar to itself. The chief microphytes are considered below; occasional tow-nettings were made from the harbour mouth to the bridge, but more often the filtering method was resorted to.

#### *Freshwater elements.*

In the course of some observations made in 1921 and 1922 on the freshwater flora of the river Rheidol, it was found that the plankton among other types was normally exceedingly scarce in this as in many neighbouring streams. The cause lay in the contamination of the headwaters of the river from waste heaps near now disused lead and zinc mines. Up to the summer of 1922, and especially after the very dry summer of 1921, it was observed that there had been a gradual increase both of species and individuals, in these rivers. I might suggest as an explanation that, as the lead mines are now closed, thus bringing no additional waste, the refuse heaps are being gradually freed by the streams, from soluble or portable mineral compounds; so that ultimately all traces of contamination from this source may vanish. There is as yet no direct evidence that this occurs. After heavy rains the amount of toxic material in the river waters, both in suspension and in solution, was greatly increased. The following are the results of some analyses made by Mr J. J. Griffiths of the Agricultural Department<sup>1</sup>:

Example No.	Name	Total solids	Zinc	Lead	Remarks
12	Ystwyth	46	nil	nil	Water clear
13	"	856	0.04	0.1	Flood time
17	Rheidol	51	nil	nil	Water clear
18	"	911	0.1	0.2	Flood time
19	"	432	0.5	Trace	Near mine
20	Clarach	640	1.6	"	" "

<sup>1</sup> *Journal of Agriculture*, 1919.

The autumn of 1922 in particular was characterised by heavy rainfall and much flooding of the low-lying lands of this district. The earlier months of 1923 also show abnormally high rainfall records, so that the increasing river vegetation of the previous years received a check. Accordingly, this drop in the freshwater vegetation would be expected in its turn to affect the freshwater organisms living in the harbour.

The greater number of such forms in the harbour was found to occur in the late summer and early autumn (Table III); this was probably because the freshwater forms attain their greatest development at that time. A favourable spot for the location of freshwater forms in the harbour was a "pocket" open to river currents rushing under the bridge, but rather more protected from tidal influences.

TABLE III. *Phytoplankton of the Harbour; Freshwater and Marine Forms.*

	Nov.		Dec.		Jan.			Feb.	Apr.	June	July		Aug.
	21	30	6	15	5	16	30	9	28	30	16	27	11
FRESHWATER													
<i>Ankistrodesmus falcatus</i>	—	—	—	—	—	r.	r.	—	—	—	—	r.	f.
<i>Closterium moniliferum</i>	—	—	r.	—	—	—	—	r.	—	r.	r.	—	r.
<i>Pediastrum baryanum</i>	r.	r.	r.	—	—	—	—	—	—	—	—	f.	f.
<i>Scenedesmus</i> spp.	r.	—	r.	—	—	—	—	—	r.	—	—	—	f.
<i>Surirella</i> spp.	r.	—	—	—	—	—	r.	—	—	—	—	—	—
<i>Navicula viridis</i>	r.	—	—	—	r.	—	r.	—	—	—	—	r.	—
<i>Tabellaria fenestrata</i>	—	—	r.	r.	—	—	—	—	—	r.	—	—	—
MARINE													
<i>Actinopterychus undulatus</i>	f.	r.	r.	r.	—	—	—	—	—	—	—	—	r.
<i>Asterionella japonica</i>	—	—	r.	—	r.	r.	r.	—	—	—	—	—	—
<i>Biddulphia mobiliensis</i>	r.	f.	—	—	r.	f.	f.	r.	—	—	—	—	r.
„ <i>favus</i>	r.	—	r.	—	—	—	r.	—	r.	—	—	—	r.
<i>Chaetoceras teres</i>	—	—	—	—	r.	r.	r.	r.	r.	—	—	—	—
<i>Coscinodiscus radiatus</i>	r.	c.	f.	r.	f.	—	—	r.	—	—	—	r.	r.
<i>Ditylium brightwelli</i>	—	r.	r.	r.	r.	—	r.	—	—	—	—	r.	—
<i>Lauderia borealis</i>	—	—	—	—	—	r.	—	r.	r.	—	—	—	—
<i>Paralia sulcata</i>	f.	f.	r.	—	r.	—	—	—	—	—	—	—	r.
<i>Rhizosolenia shrubsolei</i>	r.	r.	—	r.	—	—	—	—	—	r.	r.	—	—
<i>Skeletonema costatum</i>	r.	r.	—	r.	—	—	—	—	—	r.	—	—	—
<i>Streptotheca thamensis</i>	r.	—	r.	—	—	r.	—	—	r.	—	r.	—	—
<i>Thalassiosira decipiens</i>	r.	r.	r.	—	r.	—	—	—	—	—	—	—	—
<i>Oxyrrhis marina</i>	r.	—	—	—	—	—	—	—	—	—	r.	r.	—
<i>Thalassiothrix nitzschoides</i>	f.	f.	r.	—	f.	—	r.	r.	f.	r.	—	—	—

c.=common. f.=frequent. r.=rare.

Of the Chlorophyceae, no filamentous Conjugatae were observed to be present in a living state, but occasional filamentous forms such as *Draparnaldia plumosa* and *Ulothrix* spp. were found apparently unaffected and able to withstand being kept for some hours in the laboratory in the harbour water from which it was collected. *Pediastrum baryanum* was occasionally found on the mud after the tide had ebbed; it had well-developed marginal protuberances, presumed to be an aid to flotation. *Euglena viridis* and *Closterium moniliferum* were frequent, while *Scenedesmus* and *Ankistrodesmus* were present on the mud. Of the typically freshwater diatoms, common ones are *Tabellaria fenestrata*, *T. flocculosa*, *Navicula lata*, *N. irridis*, *N. enspidata*,

*Surirella biseriata*, *S. robusta*; while some of the rarer forms, e.g. *Meridion circulare*, were occasionally found. The curious heterokont alga *Ophiocytium arbuscula*, found in the rivers of the neighbourhood, apparently thrives in the harbour, and occurs quite frequently in the samples filtered. Of the Cyanophyceae, gelatinous patches of *Tolypothrix* sp. were sometimes found at low water. No freshwater Peridineae were found; indeed, they appear to be absent from the rivers also.

#### Marine elements.

Other things being equal, those organisms with the better flotation mechanism will tend to be floated into the harbour in greater numbers; but in the process of arriving they will have had to submit to vigorous wave action, followed by a rapid gradation of conditions from the marine to the estuarine. Most of the marine phytoplankton forms have been found alive in the harbour waters, but the fact of their existence does not necessarily prove that they thrive and multiply under such conditions.

Some plankton captured on November 30th, 1922, was placed in a wide-mouthed glass jar and secured with a cover of fine bolting silk. This was wedged in with stones at the bottom of a flight of steps on the quayside. It was hoped by this means to ascertain how far conditions of life in the harbour were favourable for prolonged growth of marine plankton. As the tide rose and covered the jar there would be renewal of water but the silk would prevent egress of the captured organisms. On the following day, some of the contents were removed for examination. *Thalassiothrix nitzschoides* was found to be fairly common, with also *Coscinodiscus*, *Chaetoceras*, *Rhizosolenia* and other plankton forms, besides freshwater forms, chiefly Chlorophyceae, and diatoms. On December 14th the remainder was taken away, and it was found that all the plankton forms were dead except *Thalassiothrix nitzschoides*, which showed evidences of active multiplication.

However, this could not be regarded as conclusive evidence either way, for the death of the plankton organisms might be due, not so much to the nature of the harbour waters, as to the fact that they were imprisoned for days under abnormal conditions of aeration and light. The success of the *Thalassiothrix* would seem to indicate its adaptability to live at any depth from a few inches to 18 feet or so below the surface; as with the inflow of the tide, the height of water over the jar increased gradually.

No Peridineae were ever found living in the harbour, and in fact only very occasionally in the littoral intertidal zone. The fact that they were apparently so extremely sensitive made it difficult to carry on observations with a view to ascertaining the cause of this; transit ashore almost invariably resulted in a curious extrusion of the plasma resembling the "cytexuviation" described by Kofoid<sup>1</sup>.

In conclusion, the main feature to be noticed in the microphytic flora of the harbour is the paucity of epiphytic and planktonic as compared with

<sup>1</sup> Kofoid. "Ceratium." *University of California Publication IV*, 1908.

benthic forms. The scarcity of the first class of organisms is due to the lack of suitable host; in the second, to the greater contrast of physical conditions with those of the inshore waters. Nevertheless, it should be noted here that Allen, in his cultural experiments on plankton diatoms found that, other things being equal, they can withstand a plus or minus 50 per cent. variation of nutrient salts in the surrounding medium<sup>1</sup>. Schimper, on the other hand, holds that the "difference between halophytes and non-halophytes is much more deeply seated in the organisation of water plants than it is in land plants<sup>2</sup>." It might therefore be considered that the intermediate estuarine conditions make for a kind of experimental ground, where the more adaptable freshwater forms may revert to a semi-halophytic mode of life, and where marine forms may develop a new habit.

#### IV. VERTICAL DISTRIBUTION.

On occasion, after the "regular" hauls were made, the net was weighted and a vertical haul made; but as it was a small net of simple pattern, and not fitted with a closing mechanism, it was difficult in this way to obtain an accurate idea of the vertical zonation in the column of water thus filtered. Furthermore, the depth over the horizontal course was only some 7 to 8 fathoms. Still, under varying conditions, the horizontal net could be made to fish in different layers of water.

One method of doing this was by weighting the mouthpiece of one net with a small lead, so that the net traversed a course some 18 inches or more below its fellow. Another device was to vary the rate of towing. With the boat going at a fair speed, the pull on the net kept it right at the surface, notwithstanding the weight of the copper ring at the mouthpiece; in these circumstances the haul was fished from the surface 2 ft. of water. When, on the contrary, the boat was allowed to drift with a fair current and a favourable wind, the net tended to fish at any depth down to the whole length of its rope. Except at slack water, the tidal streams here kept the nets usually at about 3 to 6 ft. below the surface. In this way catches could be made both of surface and of sub-surface plankton.

Where a pair of hauls were made under the conditions cited, there was nearly always a difference in volume, the sub-surface catch being usually greater than that at the surface. It should be noted that in the following examples the one exception, the catch of June 1st, was largely a zooplankton catch of Copepods:

Date	Surface c.c.	Sub-surface c.c.
3. v. 23	0.82	1.15
1. vi. 23	2.24	1.36
23. vi. 23	0.98	1.52
5. vii. 23	0.64	1.27
14. i. 24	0.23	0.39
21. iii. 24	4.9	5.5

<sup>1</sup> Allen, E. S. and Nelson. "The Artificial Culture of Marine Plankton Organisms." *Journal of the Marine Biological Association*, 1910.

<sup>2</sup> Schimper. *Plant Geography*. Oxford, 1903.

Quantitatively, also, there was often a difference so marked as to be visible to the naked eye. For instance, the surface catch of May 3rd consisted of a fine pale flocculent sediment, principally *Rhizosolenia* spp., *Thalassiothrix* and *Ditylimum*; the sub-surface haul was of a much darker colour, and showed these species less abundantly, with a preponderance of *Coscinodiscus*, *Streptotheca* and *Paralia*. Another example is that of March 21st, 1924; the sub-surface haul was of a darker hue with *Biddulphia* and *Coscinodiscus* dominant, while the lighter, yellowish tinge of the surface catch was due to a relatively greater abundance of *Rhizosolenia shrubsolei* and *Chaetoceras debile*.

While there is no hard and fast delimitation of the zones favoured by the various species, the following vertical succession would appear to exist; the difference was sufficiently great to be easily discernible on microscopic examination where the eye failed to detect any visible difference:

Surface: *Rhizosolenia*, *Ditylimum*, *Guinardia*, *Bacillaria*, *Chaetoceras*, *Thalassiothrix*.

Sub-surface: *Coscinodiscus*, *Actinopterychus*, *Biddulphia*, *Paralia*, *Asterionella*, *Lauderia*.

Bottom forms: *Pleurosigma* spp., *Surirella* spp., *Nitzschia* spp.

(i) Surface species show the greatest variation both in the life-cycle and in the external form, i.e. these species contribute largely towards the seasonal changes in the composition of the plankton. The external form is usually a development of the spinous or elongated, as for example, *Chaetoceras* and *Rhizosolenia*; the coiled forms of *Eucampia zoodiacus* and *R. stollerfothi* are noteworthy. Endochrome is a light greenish or golden yellow.

(ii) Sub-surface forms are for the most part built on bulky lines, often a development of the drum-like form. The frustules are sometimes single, as *Actinopterychus*, joined by filaments, as in *Thalassiosira*, or closely united as in *Paralia*. Endochrome is a greenish-brown.

(iii) Strictly speaking, the motile bottom forms do not belong to the plankton, except in the case of *Nitzschia closterium*, whose habit, as discussed previously, seems to partake of each phase in succession; but only after several days of dead calm is the plankton catch fairly free from these benthic forms.

## V. TEMPORAL DISTRIBUTION (PERIODICITY).

### 1. THE PLANKTON CYCLE.

The work done in this section extended over a period of 18 months, from October, 1922, to March, 1924. Even in this space of time notable variations in the phaenology of the more important plankton groups were observed, and although it might be unsafe to deduce a general yearly cycle from data collected in so limited a space of time, some attempt was made to work out a coherent sequence of plankton associations throughout that time.

(i) *Volumetric data.*

A useful, though by no means conclusive guide, is the volumetric variation in successive plankton hauls; the volume was estimated by allowing the catch to sediment in tall tubes about 10 mm. in diameter, and then replacing the same with a known volume of water. The accuracy of this method would naturally vary considerably with the nature of the catch, as forms with spines or appendages retained a much higher percentage of water in the sediment than spherical or discoid organisms such as *Noctiluca* or *Coscinodiscus*. For the same reason, any given catch when measured after a lapse of some time, was found to give a lower value; the tendency of the plankton to become shattered and much broken up resulted in their occupying considerably less space than when newly caught.

In order to lessen the already high chances of error, larger forms, such as *Pleurobrachia*, *Sagitta* or larval medusae, were removed before measuring; further, when two or more catches were made on the same date under slightly differing conditions, an average of the results has been struck. But, notwithstanding the possible, or rather probable, sources of error enumerated above, it was thought that the figures obtained bore some significance; and they are accordingly presented in Fig. 4.

"A sudden increase in the volume of the catch does not necessarily mean increase in the number of organisms prevalent at the time, or even an increase in the total number of organisms<sup>1</sup>." The quantitative values are to be taken as significant only as long as the qualitative nature of the catch is taken into consideration as well. For instance, on March 9th, 1923, there is what appears to be the normal spring increase in diatoms, but it is followed by a sudden rise in volume on March 29th. This, however, is due to an abundance of pelagic fish eggs, there being relatively few diatoms present. Thus the quantitative records alone give unreliable results, for it is less reasonable to presuppose in this case a great and abnormal drop in the number of diatoms than to attribute the same to a choking of the net with the eggs, thus impeding filtration for the obtaining of a properly representative catch.

A further example of this is shown by a consideration of the tow-net catches of the summer months of 1923. The quantitative results show a fair volume in the early months of June, with a sudden drop in July and August. Qualitative examination, however, reveals that the June abundance consisted mainly of the comparatively bulky Copepods, and that in July and August there is a great increase in Peridineae; as these are for the greater part very small forms, they give a very low volumetric value.

These two cases illustrate the necessity for supplementing comparative volumetric work with qualitative data, in order to obtain an adequate picture of the yearly plankton cycle.

<sup>1</sup> Herdman, W. A. *Journal of the Linnean Society*, 1922.



One noteworthy feature should be considered here; a comparison of the volume of the 1923 plankton catches from Aberystwyth with that of hauls made elsewhere, with the same nets and at about the same season, shows that of this district to be markedly less. As this was found to be the case when comparing with several localities, e.g. Port Erin and Menai Straits, it was concluded that Aberystwyth, and not these other areas, showed deviation from the normal (Fig. 4).

This curious circumstance developed a special interest in those cases where, although there was great difference in volume, the qualitative composition was much the same, e.g. the March and April, 1923, phytoplankton catches contained *Biddulphia* and *Chaetoceras* spp. respectively in much the same proportions both for Aberystwyth and for the corresponding other district, but the Aberystwyth catch in each case is lower.

I suggest in explanation of this, a hypothesis following the lines of W. H. Pearsall's theory of diatom periodicity (8). He states that the factor limiting diatom periodicity is deficiency of oxygen, nitrates, silica, or calcium; the spring and autumn river floods remove much terrestrial material in solution, chiefly nitrates and phosphates. He shows also that increased nitrate content of the river waters is correlated with a similar increase in silica. "Lowered salinity is certainly due to the discharge of flood waters by the river, and since the average freshwater has a much higher nitrate and silica content than has the sea, it may be assumed that lowered salinity is normally correlated with higher dissolved nitrates and silica in the sea water" (*loc. cit.*).

The particular application here is that river floods have been proved to bring down a greater quantity of lead and zinc compounds, chiefly as minute particles in suspension, though with a small amount in solution. Now most algal forms are extremely sensitive to even infinitesimal quantities of metallic salts in solution, so that vegetation in these rivers is extremely scanty; whether the river waters discharged into the sea are sufficiently toxic to affect the plankton diatoms adversely would have to be proved by actual experiment; but this is certain for the Aberystwyth waters, that the very fluvial influences which tend to promote diatom growth with the increased nitrate and silica content, bear at the same time an increased toxic charge of lead and zinc compounds.

At all events, the following would seem to furnish corroborative evidence. The usual September–October diatom maximum for 1922 was delayed until November–December of that year, when *Chaetoceras* spp. and *Thalassiosira* were abundant. Correlated with this is the fact that September in this district was characterised by heavy rainfall and much flooding; October and November, on the contrary, were abnormally dry, and December very dry, thus allowing for a delayed but well-represented autumn maximum<sup>1</sup>.

<sup>1</sup> It is noteworthy that the flowering period of many terrestrial plants was delayed some six or eight weeks in this district.

To take a second example, the early months of 1923 were characterised by high seas and an abnormally high rainfall, thus swelling the rivers; the

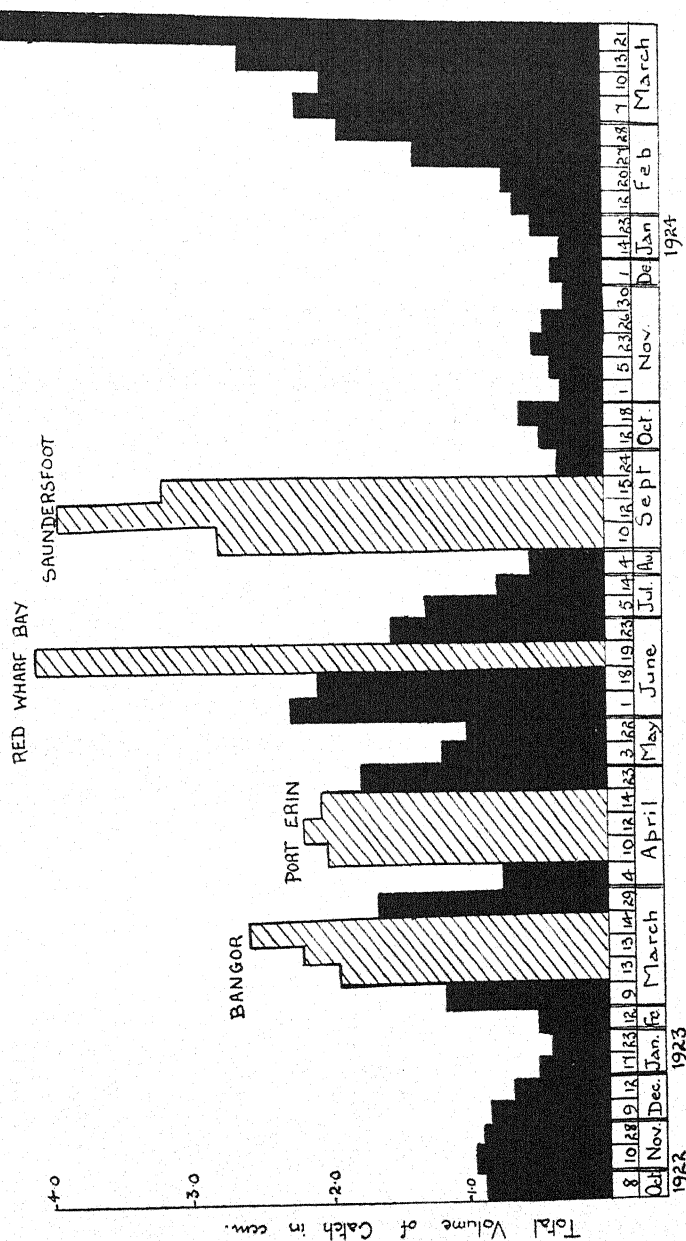


FIG. 4. Volumetric variation in plankton. Aberystwyth values given in black.

prevailing winds, too, were from the S.W., driving the contaminated waters of the Rheidol northwards along the coast. At the same time, the volume of the plankton was at its lowest. Contrast these conditions with January and

February of 1924, characterised by clear seas, low rainfall, and prevailing N. and N.E. winds; here the plankton volume rose slowly till mid-February, and then increased very quickly. Possibly, indeed, the whole of the 1923 plankton may be considered to be somewhat deranged owing to the abnormal meteorological conditions which prevailed then.

(ii) *Composition of the phytoplankton.*

Plankton organisms are classifiable according to their group habit as follows:

By far the greater number of plankton species have a period of maximum development at one or two biological seasons during the year. Most genera attain their maxima at a period between March to June, with sometimes also another growth period in late autumn. A second and less important group comprises those forms which are constant components of the plankton flora, but which are never found so abundantly as to affect quantitative values. Such forms usually occur in very small numbers, e.g. *Stephanopyxis turris*, *Ceratium tripos* (though this latter is recorded as abundant in the summer at Port Erin). Thirdly, we have those species which occur at intervals throughout the year in an apparently anomalous manner, though they sometimes seem spasmodically abundant, e.g. *Streptotheca thamensis*.

(iii) *Phytoplankton phases.*

The periodicity figures upon which most of the conclusions arrived at were based, were obtained by a method of estimation to be described in the writer's forthcoming paper on technique. These data were tabulated and a cycle of the yearly phases constructed. A detailed account of the plankton flora month by month is given below, but some preliminary observations as to the seasonal succession of the various ecological units will first be given. For Aberystwyth, four seasonal phases can be recognised:

(a) The spring phase is by far the most important as far as the phytoplankton is concerned; three distinct stages can be observed. Firstly, there is a sudden rise in February–March, with an increase in *Biddulphia regia* and the larger Coscinodisci—*C. concinnus*, *C. grani* and *C. sub-bulliens*. The smaller form *C. radiatus*, with also *B. mobiliensis*, have been present throughout the previous phase, and persist for some time undiminished. The spring Coscinodisci and *B. regia* bulk large in the plankton; both forms are easily visible to the naked eye. There is also a great abundance of *Bacillaria paradoxa*, with some slight increase in the number of such forms as *Lauderia* and *Rhizosolenia*. The 1923 *Biddulphia*-phase came quite late in March, but in 1924 the rise began in mid-February.

Secondly, this *Biddulphia*-maximum was overlapped by the April *Chaetoceras*-phase, consisting almost entirely of species of this genus, chiefly *Ch. debile*, *decipiens*, *danicum*, *curvisetum*, *densum* and *teres*.

Thirdly, this *Chaetoceras*-phase gives way in early May to abundant *Rhizosolenia semispina* and *R. shrubsolei*, followed by an increase in *Guinardia flaccida* and *R. stollerfothi* in June. Zooplankton is abundant from this month onwards.

(b) The summer phase is short in duration, with scarcely any diatoms, and a moderate amount of zooplankton. Dinoflagellata are quite frequent, but by no means abundant. They began in mid-July with the occurrence of some northern oceanic forms as *Ceratium longipes*, *C. intermedium* f. *frigida*, and gave way in early August to an abundance of the smaller Peridineae, chiefly *Peridinium* spp., *Gonyaulax*, *Diplopsalis* (and its derivatives), and *Dinophysis* in small numbers.

(c) The autumn phase is characterised by a second increase in diatoms, but it is a smaller and apparently more erratic increase than that of the spring phase. Herdman states that "the secondary lesser maximum in autumn...is very variable both in extent and in constituent organisms" (3).

*Chaetoceras* is the typical genus, and the 1922 autumn phase here in November–December certainly showed an abundance of *Chaetoceras* spp., with also *Thalassiosira*. In 1923, however, there is a very scanty indication of the diatom increase, and this is attributable to *B. mobiliensis* and *C. radiatus* rather than to *Chaetoceras* itself. In fact, both the spring and autumn 1923 *Chaetoceras*-phases seem to be somewhat erratic in the Aberystwyth records. Compare the poor autumn development here with the Saundersfoot records, a contrast best seen by referring to Fig. 4.

(d) The winter phase is a "monotonic" phytoplankton, consisting principally of *Biddulphia mobiliensis*, *Coscinodiscus radiatus*, *Thalassiothrix*, *Paralia* and *Actinopterychus*. The total volume is always small. A point of interest is that, just at the minimal development of the two winter phases, there is a brief but striking "swarming" of *Ceratium* spp.; *C. fusus* on January 17th, 1923, and *C. furca* on November 1st, 1923, the latter being followed by an abundance of *Prorocentrum micans*. It was found that in the latter case, the swarm had almost disappeared by November 5th.

The above phases are graphically represented in Fig. 5.

#### 1922. (iv) *Analysis of the plankton flora.*

*October.* *Chaetoceras* spp. and *Thalassiosira* spp. frequent, with also *C. radiatus* and *B. mobiliensis*; *Asterionella* and *Ceratium fusus*, *Skeletonema* and *Paralia* present in small numbers. Few Copepods.

*November.* As above.

*December.* *Ch. curvisetum*, *didymum*, *decipiens* and *teres* still present, but decreasing in numbers. Occurrence of some forms rare for Aberystwyth, e.g. *Bacteriastrum varians*, *Stephanopyxis turris*; possibly traces of a winter invasion from oceanic waters.

#### 1923.

*January.* Decrease in diatoms, delayed winter minimum; *Actinopterychus*, *C. radiatus*, *B. mobiliensis* and *Thalassiothrix*; *Ceratium fusus* swarm.

*February.* As above.

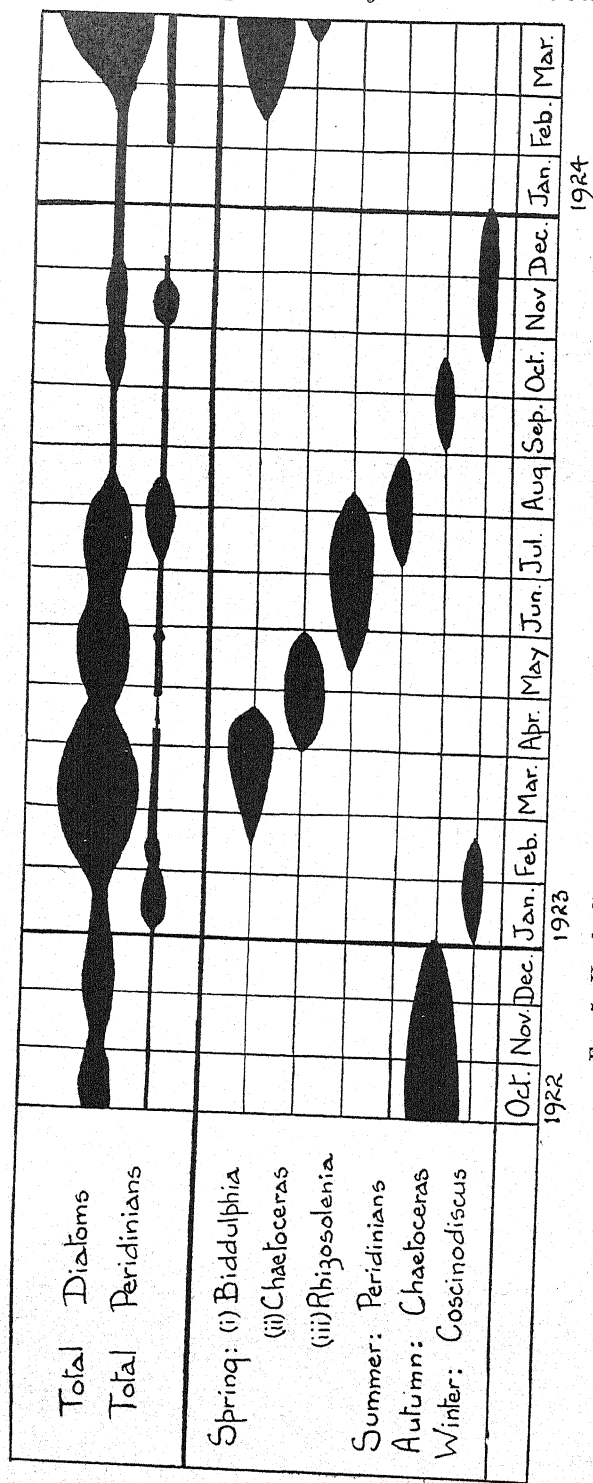


FIG. 5. Yearly distribution of the principal phytoplankton phases.

*March.* Increase in *Biddulphia regia*, *Bacillaria*, *Coscinodiscus grani*, *C. sub-bulliens*, *C. concinnus*; the winter diatoms still frequent. Abundant pelagic fish eggs on the 29th. Mid-March tow-nettings at Bangor showed a much greater volume, with abundant *B. sinensis*, *Eucampia zodiacus*, *Balanus nauplii* and larval stages of Copepods and Ostracods. Red Wharf Bay (28th) principally of *Thalassiothrix*.

*April.* The *Chaetoceras*-phase, though this genus itself is not well represented; *Lauderia*, *Thalassiothrix* present. *Biddulphia* decreasing; *Rhizosolenia* and *Guinardia* increasing. Tow-nettings at Port Erin gave a somewhat greater volume with more abundant *Chaetoceras* spp., *Eucampia* and *Fragilaria*.

*May.* Slight drop in volume; *Bacillaria*, *Biddulphia* and *Chaetoceras* in small numbers; *Rhizosolenia shrubsolei*, *R. styliformis*, *R. setigera*, *R. semispina* and *Thalassiothrix* frequent. *Halosphaera*; small Peridineae with also some zooplankton. *Phaeocystis* on the 22nd.

*June.* Great abundance of *Guinardia*, with *Rhizosolenia* spp., chiefly *R. stollerfothi*; *Halosphaera*; small Dinoflagellata increasing: *Prorocentrum micans*, *Peridinium* spp. and *Diplopsalis*. Some *Ceratium intermedium*. Copepods dominant at the beginning of the month.

Red Wharf Bay has abundant *Guinardia* and *R. stollerfothi* with a *Noctiluca* swarm.

*July.* Considerable decrease in volume; fewer diatoms and Copepods, but the small Peridineae are abundant.

Late June and July oceanic in general character, with a slender form of *Ceratium furca*, *Dinophysis* spp. and the large Copepod *Calanus finmarchicus*.

*August.* Decrease in Peridineae; *P. micans* in small numbers. *Distephanus speculum*; diatoms reappear, with *Biddulphia mobilensis*, *B. rhombus*, *Bacillaria* and *Bellerophon*.

*September.* Slight increase in the above, with also *Coscinodiscus radiatus*, *Actinopteryx* and small numbers of *Chaetoceras* and *Rhizosolenia* spp.

Tow-nettings at Saundersfoot showed abundant *Chaetoceras*, *Thalassiosira* and *Thalassiothrix*; *Biddulphia alternans*.

*October.* Slight increase in volume, but more characteristic of the winter phase, with *C. radiatus* and *B. mobilensis*.

*November.* As above; winter minimum. Swarm of *C. furca* and *Prorocentrum micans*.

*December.* As above.

1924.

*January.* Increased volume; *Lauderia*, *Rh. semispina*.

*February.* Slow rise at beginning of month; about the 20th a sudden development of *B. regia*, *Bacillaria*, and the larger *Coscinodiscus* spp.; some *Chaetoceras* and *Rhizosolenia*. A few larval zooplankton organisms; *Sagitta* frequent.

*March.* Great increase in volume; *Biddulphia*-maximum towards middle of the month; increase in *Chaetoceras debile* and in *Rhizosolenia semispina* towards end of month.

## 2. PHAENOLOGY OF THE CHIEF SPECIES.

Different genera and even different species of the same genus may have their period of maximal development at different seasons. It has been shown in the foregoing paragraphs that a classification of the phytoplankton is possible, into groups whose members have their maxima at the same biologic season. Any cause which tends to delay or inhibit any one form will tend to affect in a similar manner all the other forms in that phase also. The following account of their phaenology was deduced from the result of the tow-net hauls, supplemented in the summer months by centrifuging water-samples.

## DIATOMS.

- Actinopterychus undulatus*. Present through winter months, moderately abundant towards February; disappears April to May, reappearing in August.
- Asterionella japonica*. In small numbers October to May; spiral form frequent.
- Bacillaria paradoxa*. Small numbers October to early February, c. February and March; absent April to August. Follows *B. regia* closely.
- Bacteriastrium varians*. Very rare; occasional individuals December to March.
- Bellerophon malleus*. Rare; October to January; apparently an autumn form only.
- Biddulphia alternans*. c. September, Saundersfoot; absent from Aberystwyth.
- B. javus*. January to March; August to October.
- B. granulata*. January to March; August to October.
- B. mobiliensis*. Frequent September to May; maximum March; present in very small numbers through the summer.
- B. regia*. October to April; maximum February to March. The allied species *B. mobiliensis* has a longer range over the biological year.
- B. rhombus*. Fairly frequent August and November.
- B. vesiculosa*. August to October; January to February. This species, with also *B. rhombus* and *B. javus* is usually restricted to the littoral inshore waters.
- Cerataulina bergoni*. September–October and February–March; r.
- Chaetoceras boreale*. October to December and March to April.
- C. curvisetum*. October to January and April to May; c.
- C. contortum*. r.r. August to October; c. March and April.
- C. crinitum*. March to April and September to October; an early species of *Chaetoceras*.
- C. convolutum*. An early species; March to April and September.
- C. danicum*. March to May and October to December; maxima in April and October.
- C. debile*. Earliest spring *Chaetoceras*; early March to May; August to November.
- C. decipiens*. August to November, March to May.
- C. densum*. r.r. October to December; frequent April.
- C. didymum*. Frequent November to December; r. April.
- C. lacinosum*. October to December, April to May.
- C. schutti*. Frequent April to May; also present November to December.
- C. sociale*. r.r. February to April; c. September at Saundersfoot.
- C. simile*. r.r. April to May and September.
- C. pseudocrinitum*. r.r. April.
- C. teres*. Frequent September to December; c. early March to April; one of the commonest species.
- C. Willei*. r.r. September to December and March to April.
- Corethron hystrix*. One individual only, December, 1922.
- Coscinodiscus concinnus*. August to October, January to May; maximum March.
- C. excentricus*. January to April, September to November; not common.
- C. granii*. October to December and January to April; maximum March.
- C. radiatus*. Present throughout the year except June and July; is typically developed in the winter months; maximum in January.
- C. sub-bulliens*. Present February to April.
- Coscinosira polychorda*. Occasional individuals December to February.
- Ditylism brightwelli*. Present October to December in small numbers; frequent March to June.
- Eucampia zodiacus*. Maxima March and September, Bangor and Saundersfoot respectively; r.r. Aberystwyth.
- Fragilaria oceanica*. r.r. July.
- Guinardia flaccida*. March to July; maximum June.
- Hyalodiscus stelliger*. c. January to March.
- Lauderia borealis*. February to April; maximum March.

- Leptocylindrus danicus*. Frequent March to April; absent other months.  
*Nitzschia closterium*. February to June; maximum May.  
*Rhizosolenia stollerfothi*. January to July; maximum June.  
*R. shrubsolei*. October to June; maximum May to June.  
*R. semispina*. November to May; not very common.  
*R. setigera*. r.r. January to May.  
*R. styliformis*. October to December and May; frequent.  
*Skeletonema costatum*. August to October, January to May; maximum May.  
*Stephanopyxis turris*. r.r. December to January, but c. September, Saundersfoot.  
*Thalassiosira gravis*. r.r. October to November and January to mid-March; frequent November, 1922, also September, 1923, Saundersfoot.  
*T. nordenskioldii*. c. September, Saundersfoot; absent Aberystwyth.  
*T. condensata*. As *T. nordenskioldii*.  
*Thalassiothrix nitzschiioides*. Present all the year except June and July; maximum January.  
*Paralia sulcata*. Frequent December to May; August to October.

#### DINOFLAGELLATA.

- Ceratium tripos*. Usually only r. but often present in the hauls, March to September; maximum July.  
*C. batavum*. r.r. July and August.  
*C. intermedium* f. *frigida*. Frequent June to July.  
*C. fusus*. Present in small numbers all the year; maxima February, August and November, 1922.  
*C. farca*. January to March, September to November.  
*Diplopsalis lenticula* (and allied forms). July to September; few individuals March to June.  
*Dinophysis acuta*. r.r. July and August.  
*D. rotundata* (*Phalacroma rotundata*). r.r. July and August.  
*Peridiniopsis asymmetrica*. May to September; maximum July to August.  
*Gonyaulax spinifera*. March to September; fairly frequent.  
*Peridinium conicum*. r.r. July.  
*P. depressum*. February to August.  
*P. divergens*. February to August.  
*P. ovatum*. May to August.  
*P. pallidum*. r.r. August.  
*P. pellucidum*. r.r. August.  
*P. Steini*. r.r. August.  
*Prorocentrum micans*. r.r. July and August, but c.c. in tow-net catches November 1st and 5th, 1923.

#### PROTOPHYTA CETERA.

- Distephanus speculum*. r.r. July and August, but present October.  
*Halosphaera viridis*. May to June; c.  
*Phaeocystis* spp. r.r. April to June.  
*Ocyrrhis marina*. May to August.  
*Trochiscia* sp. r.r.

#### ZOOPLANKTON.

I am indebted to Mr E. E. Watkins, Zoology Department, for much help with the identification of the zooplankton forms. These are practically absent in the winter, increasing in spring with *Balanus nauplii*, *Pluteus* larvae and larval stages of Copepods and Ostracods. The end of March, 1923, had abundant pelagic fish eggs; in 1924, at the maximum of the *Biddulphia*-phase, the



Copepod *Cyclops* was most frequent. April and May had comparatively little zooplankton, but Copepods were dominant in early June. The July oceanic waters brought in the large Copepod *Calanus finmarchicus*; postlarval fish stages and hydromedusae were quite common in this month too. *Pleurobrachia pileus*, *Sagitta bipunctata* and *Noctiluca miliaris* occurred in small numbers from March to September. Whiting and herring were fished in the bay, but in 1923 there was no mackerel.

### 3. NANNOPLANKTON.

It is known that many of the very minute plankton organisms are lost with even the finest-meshed nets; they are so small as to pass easily through the mesh, and are only captured when entangled on the threads of the silk, or among the spines and setae of the larger forms. This loss of plankton has been variously computed by different observers as being from 2 to 50 per cent. In the summer months of 1923, therefore, the tow-net catches were supplemented by centrifuging water-samples.

Table IV enumerates those organisms centrifuged from 60 c.c. of sea-water, the water-samples being taken about  $1\frac{1}{2}$  miles from shore, at the time of the "regular" tow-nettings. It will be seen that, of the nannoplankton, the greater proportion are the small Peridineae; the very small plankton diatoms are

TABLE IV. *The Nannoplankton of the Summer Months.*

	March	April			May		June		July		Aug.	
	29	4	5	23	3	22	1	18	5	14	4	18
DIATOMS												
<i>Biddulphia mobiliensis</i>	4	1	—	—	1	—	—	—	—	—	—	1
<i>Rhizosolenia stolterfothi</i>	—	—	—	—	1	3	—	2	—	—	—	—
„ <i>shrubsolei</i>	—	2	1	—	1	—	—	—	1	—	—	—
<i>Guinardia flaccida</i>	—	—	—	1	1	3	2	7	—	1	—	—
<i>Cerataulina bergoni</i>	—	—	—	1	—	1	—	1	—	—	2	—
<i>Chaetoceras boreale</i>	—	—	1	—	2	2	3	—	—	—	—	—
<i>Thalassiothrix nitzschoides</i>	—	—	—	3	—	1	1	—	—	—	—	—
PERIDINIANS												
<i>Dinophysis acuta</i>	—	—	—	—	—	1	1	3	1	2	—	—
„ <i>rotundata</i>	—	—	—	—	—	—	—	1	—	—	—	—
<i>Gonyaulax spinifera</i>	—	—	—	—	—	1	—	6	2	—	—	—
<i>Diplopsalis lenticula</i>	—	—	2	—	—	4	1	3	3	2	2	—
<i>Peridinium conicum</i>	—	—	1	—	2	—	3	—	1	—	—	—
„ <i>depressum</i>	—	—	—	—	—	3	3	2	4	1	—	—
„ <i>divergens</i>	1	1	—	—	2	1	3	2	13	9	1	—
„ <i>ovatum</i>	—	—	—	—	—	—	—	1	—	1	—	—
„ <i>spp.</i>	—	2	—	1	—	—	4	1	1	—	4	—
<i>Prorocentrum micans</i>	—	—	1	—	1	—	2	—	1	1	—	1
PROTOPHYTA CETERA												
<i>Distephanus speculum</i>	—	—	—	—	—	—	—	—	—	—	—	1
<i>Acanthometron pellucidum</i>	—	—	—	1	—	—	—	—	—	1	—	—
<i>Halosphaera viridis</i>	—	—	—	1	—	1	—	—	—	—	—	—
<i>Oxyrrhis marina</i>	—	—	—	—	—	—	—	1	—	5	1	—
<i>Trochiscia</i> sp.	—	—	—	—	—	—	—	—	1	—	—	1

(Numbers in 60 c.c. of sea-water.)

represented by *Skeletonema* and *Nitzschia closterium* in particular, but, as the centrifuging work was done in the summer months when diatoms were scarce, they cannot be considered as adequately represented here. The greatest development of nannoplankton is in the summer months, when *Peridinium* spp., and *Diplopsalis* and its allies are at their highest. *Gonyaulax* is present in small numbers from the tow-nets from February onwards, and *Prorocentrum micans* is abundant as late as November; *Dinophysis* is confined to the mid-summer records.

Of the protista, *Distephanus speculum*, *Oxyrrhis marina*, *Acanthometron pellucidum*, *Trochiscia clevei* and several unidentified Cryptomonad forms were recorded from the water-samples; no Coccolithophoridae were observed, except in May, when a unicellular brown xanthella-like organism was found.

*Halosphaera* was found in the water-samples, as well as in the tow-net catches, but it should be noted as a curious fact that the large phytoplankton forms such as *Biddulphia*, are relatively much less common in the water-samples than contemporaneous tow-net evidences would seem to warrant. Furthermore, no sample was found to collect any larger zooplankton forms such as *Pleurobrachia*. It would seem therefore that the smaller the water-sample taken, the less are the chances of capturing the larger forms. Table 4 also shows that the small Peridineae noted as rare in the tow-net catches are quite numerous in the water-samples, and are found to be sedimented by the centrifuge when not recorded at all from the tow-net.

Wherever possible, the derivatives of *Diplopsalis lenticula* were identified according to the recent researches of Dr Lebour (7), but the difficulty of preliminary clearing for evaluation of the plate formula, together with the small amount of material available for examination, rendered this a matter of some uncertainty. Where the identity of such forms was doubtful, they were referred to *Diplopsalis*. For the genus *Peridinium*, Paulsen's classification in *Nordisches Plankton* (2) was employed.

These nannoplankton records were somewhat cursory, but it is hoped to make a fuller study of these interesting forms during the summer of 1924.

## VI. COMPARISON WITH OTHER PLANKTON RECORDS.

The frequency records obtained during the past 18 months are on the whole very similar to the 1905 results of Gough and Bygrave for Cardigan Bay. There are, however, some slight differences for the maxima of the successive yearly phases. As in these records, the *Biddulphia*-phase comes in early spring with a lesser maximum in September. The spring *Chaetoceras*-phase of 1905 is delayed till June, with a corresponding delay of *Rh. shrubsolei* to August. *Rh. stolterfothi* is only r.r. in the 1905 table, whereas it was common in June of 1923. In both these periods the autumn phase is characterised by a poor development of *Chaetoceras*.

With regard to the Dinoflagellata, both years show a *Peridinium-Diplopsalis* maximum in August, with also *Ceratia* of the *tripos*-type; however, 1905 has a *C. furca* and *C. fusus* maximum at the same time, whereas 1922-4 has a sudden winter development of these species—*C. fusus* in the first winter phase, and *C. furca* in the second.

Certain forms found fairly frequently elsewhere were only occasional in this area both in 1905 and in 1922-4. *Thalassiosira* spp., *Coscinosira polychorda*, *Eucampia zodiacus* and *Bellerochea malleus* are chief among these. *Biddulphia sinensis* also has been observed on a few occasions only; it is naturally not represented in the records of Gough and Bygrave, as its migration (thought to be accidental) from the Indian Ocean to North European seas did not take place till 1903; and it was first recorded for British waters in 1909. The occurrence of *Eucampia* along the Welsh coasts seems to be somewhat erratic. Riddell notes<sup>1</sup> that "its complete absence from our Carnarvon Bay records is rather puzzling, unless we suppose that here too the flowering period was later than September. On the contrary, it occurred in fair quantities in the south of Cardigan Bay on May 21st." Here it is only very occasionally present, and then only r.r., although it was quite abundant for Bangor in March, Port Erin in April, and Saundersfoot in September, 1923.

A suggested explanation for the rarity of these forms here is as follows:

In comparison with plankton records for elsewhere along the Welsh coast, it would seem that Cardigan Bay possesses an indigenous flora comprising most of the outstanding phytoplankton species; the rarer species would then tend to occur only with an invasion of currents from outer waters, and even then in small numbers only. Herdman states that midwinter and midsummer are more oceanic in character than other times of the year; this seems to be the case here, for November-December and July-August are the two periods in which such epidemic forms as *Bacteriastrium* and *Bellerochea* are apt to occur.

In contrast to this is the fact that *Coscinodiscus radiatus*, *Paralia sulcata* and *Thalassiothrix nitzschoides* are typically winter forms, but are present in small numbers throughout the year; Gough's theory of the distribution of neritic diatoms is that they occur at definite times only, in places near the ocean, "but stay all the year round in suitable localities far removed from it" (6). With regard to those forms which are rare here, it is therefore suggested that conditions in this particular sea area were initially unsuitable, and further that the bathytopographical conformation of the bay militates against a too easy incursion of forms brought in by oceanic currents.

The March, 1923, tow-nettings from Red Wharf Bay and the Menai Straits, besides being appreciably greater in volume, are considerably richer in *Biddulphia sinensis*, *Eucampia*, *Fragilaria* and *Thalassiosira* spp., when com-

<sup>1</sup> Riddell. "Plankton of Periodic Cruises." *Report of the Lancashire Sea Fisheries Laboratory*, 1913.

pared with the Aberystwyth spring phase of that year. That of 1924 shows a greater volume, but is still lacking in those forms listed as epidemic for this district. Similarly, a comparison of the September, 1923, "regular" tow-nettings with those from Saundersfoot in the same month, shows the latter to have a much greater volume, with more abundant *Chaetoceras debile*, *densum*, *danicum*, *decipiens*, *teres*; there are also present *Thalassiosira gravida*, *decipiens*, *condensata*, *Eucampia*, and a form not found elsewhere along the Welsh coasts, namely, *Biddulphia alternans*. It occurred in fair abundance. Judging from this one series of tow-nettings, this bay on the Bristol Channel appears to be particularly favourable for the development of phytoplankton.

With the above reservations as to the absence of certain species, the same general yearly course as that of the Port Erin records was found to hold good; it is stated in the 1906 reports "that the distinction between the constituents of the plankton of the Welsh and Lancashire coasts is very marked."

From observations extending over a long period of years, Herdman places the *Biddulphia*-rise at March-early April, with *Chaetoceras debile* in late April, *Ch. sociale* in May with *Thalassiosira* spp. and *Lauderia*; and *Guinardia* and *Rhizosolenia* spp. in June. *Ch. sociale* is not nearly so frequent here, and *Ch. boreale* seems to have a wider range over the biologic year; Herdman states that it does not appear in the Irish Sea till May. Here, as there, *Rhizosolenia* spp. develop in the order *semispina*, *shrubsolei*, *stolterfothi*, but the former is not very common, and the latter is practically confined to a brief development in June.

With regard to the Dinoflagellata, *Ceratium tripos* and tripos-forms are not at all common here, whereas at Port Erin they are recorded as having a fairly important summer maximum. This is perhaps not surprising, as the Irish Sea is much more open to northern oceanic influences distributing the summer "tripos-plankton" of Cleve. For a similar reason the "sira-plankton" of the earlier months of the year at Port Erin, with *Thalassiosira decipiens* and *Th. nordenskioldi*, is well-developed; whereas Cardigan Bay, being less accessible to these influences, has only very occasional individuals of these species. The "tricho-plankton" or winter phase, with *Ch. boreale*, *Ch. decipiens*, *Biddulphia mobiliensis*, *Coscinodiscus* and *Rhizosolenia* spp., is present for this district also; and there is a similar spring or "didymus" phase consisting mainly of *Chaetoceras* spp.

It should be noted that there was a 1923 summer oceanic invasion for Aberystwyth, with *Dinophysis* spp., *Ceratium intermedium* and smaller Peridineae.

The Aberystwyth plankton appears to resemble that of the Plymouth records very closely. With regard to the diatoms, however, *Skeletonema* seems to be much more abundant there than here; this is perhaps due to the fact that the tow-nets missed many such small forms. *Rh. stolterfothi* is recorded as the commonest *Rhizosolenia* sp. at Plymouth, whereas Aberystwyth

resembles Port Erin in having more abundant *Rh. shrubsolei*. Dr Lebour records several sp. of *Thalassiosira*. *Thalassiothrix* and *Coscinodiscus radiatus* occur practically all the year round here, but at Plymouth, the former in particular, is "a pronouncedly winter form"; *Bacillaria*, on the contrary, is present there in small numbers throughout the year, but here it follows *Biddulphia regia* closely in its distribution through the year. The occurrence of *Dinoflagellata* is much the same in both cases; *Ceratium tripos* is only occasional, and *C. fusus* is practically the only winter peridininian.

Lohmann's figures for Kiel (Steuer) show much the same diatom curve, but here again there is a strikingly less-developed *Skeletonema*-phase for Aberystwyth; at Kiel it begins to increase in March, is equally abundant with *Chaetoceras* spp. in April, and is the dominant form in June. There, as also in the Irish Sea records, *Ceratium* is abundant from June to November, with a maximum in August.

A special point brought forward by Steuer is the progressive hastening of the spring maximum, with a corresponding delay of the autumn maximum as we progress southwards. "Je weiter wir nach suden vorschreiten, desto früher tritt das Frühlingsmaximum, desto später das Herbstmaximum ein<sup>1</sup>." There is no considerable range of latitude in British waters for local application of this, but when compared with records for the north and south coasts of France, it is well borne out. The Port Erin maxima are in March and September; those of Plymouth are in April and October; Mangin gives them as March-May and October-December for St Vaast la Hougue, Pas de Calais; while Pavillard records from Golfe de Lyons maxima in February and November, with also a few diatoms in June.

In conclusion, I wish to tender my acknowledgments to the Department of Scientific and Industrial Research for enabling me to take up this work. In addition to assistance received from persons mentioned in the text, and gratefully acknowledged here, I am greatly indebted to Mr S. G. Jones, M.Sc., for much help, and to Prof. J. Lloyd Williams, D.Sc., for the criticisms and assistance afforded me throughout the course of the work done.

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# ON THE ECOLOGY OF THE VEGETATION OF BRECKLAND

By E. PICKWORTH FARROW.

## VIII. VIEWS RELATING TO THE PROBABLE FORMER DISTRIBUTION OF *CALLUNA* HEATH IN ENGLAND.

(With one Figure in the Text.)

*CALLUNA* heath alternates with grass-heath in Breckland, and this was previously supposed to be probably due to varying proportions of lime in the associated soils—some of the grass-heaths approach chalk pasture in the character of their vegetation and the soils frequently contain appreciable quantities of lime.

As described in Part II<sup>1</sup>, it was discovered however that many of these grass-heath areas arise by the degeneration of typical *Calluna* heath owing to biotic attack on the *Calluna*. This process of degeneration of *Calluna* heath to grass-heath occurs in many localities in Breckland and is a widespread phenomenon in this district. The process has probably been going on for some time and many areas now grass-heath were doubtless once typical *Calluna* heaths before they were rabbit attacked or grazed so heavily as they are at present.

Many things indicate that Higham Heath, which lies on the south-west border of Breckland, and which is now a pure grass heath, was very probably once a typical *Calluna* heath. Some plantations of gorse bushes have been made on Higham Heath but these are degenerating rapidly at their edges owing to the rabbit attack and to grazing by sheep. Some planted gorse bushes occur on Cavenham Heath and they do not degenerate so rapidly as the *Calluna*. Thus if gorse degenerates rapidly on Higham Heath, *Calluna* would have degenerated more rapidly, under comparable biotic attack. The absence of *Calluna* now is no evidence that it was never there.

*Rumex acetosella*, indicative of acid surface conditions, occurs on Higham Heath. *Calluna* is not intolerant of a high lime content below the surface layers of soil, provided other conditions are favourable, but heavy biotic attack by sheep or rabbits or both has been shown to be extremely antagonistic to its persistence.

Remarkable mixed communities termed "chalk-heaths" and "limestone-heaths" sometimes occur on soils overlying calcareous materials. These are characterised by a mixture of typical heath and typical limestone plants.

<sup>1</sup> This JOURNAL, 4, 1916.

The surface layers of undisturbed soils overlying calcareous rocks are typically extremely poor in lime although the lower layers of the soil are usually rich in lime. Various writers have recorded that *Calluna* can colonise the superficial layers poor in lime over calcareous rocks if the other conditions are favourable and it appears that these other conditions would include the absence of heavy biotic attack. If *Calluna* could once colonise the superficial layers, dead *Calluna* leaves would eventually fall on the surface and the typical subordinate vegetation of mosses and lichens would gradually decay so that eventually a considerable thickness of peat or peat-like substance would form over the superficial layers of soil overlying the calcareous rock, and typical *Calluna* heaths on superficial peat might eventually be produced, as is actually the case on many limestone and chalk plateaus.

Possibly extensive areas in England on certain soils may have been formerly occupied by *Calluna* heath after the degeneration of the primitive woodland from preliminary pasturing where the latter was not sufficiently severe to cause the *Calluna* heath type of vegetation to degenerate. "Chalk-heath" and "limestone-heath" communities may perhaps often represent attempts on the part of *Calluna* and its associates to colonise the most favourable portions of their former distribution area where surface layers are poor in lime when the intensity of the local biotic attack becomes temporarily sufficiently reduced.

It would be well to test this theory of the origin of "chalk-heath" and "limestone-heath" communities through locally reduced biotic attack by means of erecting grazing- and rabbit-proof enclosures in various places in such communities and noting the resulting effects. It may very likely be found that the protected areas will develop typical *Calluna* heath after the grazing pressure has been removed.

There are areas of grass-heath between Barton Mills and Newmarket the soils and grass vegetation of which resemble those of Cavenham Heath: fragments of species of *Cladonia* occur. It is very possible that these heaths were formerly *Calluna* heaths before the biotic attack of grazing animals was as heavy as it is at present.

There is in fact a series of areas called "heaths" running across this part of the country on the chalk of the "East Anglian Heights," viz. the Breckland Heaths (including Higham Heath), Newmarket Heath, and Royston Heath. These "heaths" become increasingly like chalk *pasture* as one passes from the Breckland Heaths to Royston Heath. "The tracts of country occupied by this (grass-heath) association are often called heaths, although the true heath plants (*Calluna*, *Erica*, etc.) may be entirely lacking, but all transitions are found between the grass-heaths and the *Calluna* heaths...." "This term ('heath') is even used in East Anglia for tracts of chalk pasture, e.g. Royston Heath, Newmarket Heath<sup>1</sup>."

<sup>1</sup> *Types of British Vegetation*, p. 95.

When the primitive woodland degenerated (probably chiefly owing to early pasturing) large open spaces bare of trees resulted, and when these were uncultivated they were termed "heaths." What are now known as "heath plants," such as *Calluna*, *Erica* and their associates, were probably highly characteristic of these "large open areas bare of trees" (resulting from the degeneration of woodland) which were termed heaths.

It is quite possible that Newmarket "Heath" and Royston "Heath" may once have been occupied by the typical heath vegetation on a layer of peat after the degeneration of the primitive woodland and before the biotic attack was as heavy as it is at present<sup>1</sup>. It is very possible also that many areas of the chalk where the superficial layers are poor in lime may once have been occupied by typical *Calluna* heath before the biotic attack was as heavy as it is now.

In this connection it is interesting to note that Mr A. G. Tansley and Mr R. S. Adamson have found *Calluna vulgaris* colonising, flowering and reproducing by seed inside one of their rabbit-proof enclosures on fairly typical chalk down at Ditcham Park on the Hampshire-Sussex border<sup>2</sup>.

Mr Tansley has also informed the writer of some interesting phenomena which he observed in 1916 on the northern face of Moel Siabod in North Wales.

A stone wall runs along the mountain side at a height of 1700 feet above sea level. Below the wall there is a great deal of vigorous *Calluna*—indeed it is generally dominant—while in general there is no *Calluna* above the wall although the soil and slope conditions are just the same.

Many sheep are pastured on the area above the wall, which is a common grazing ground, while only a few sheep are occasionally pastured below the wall.

The stone wall has become ruined so that sheep can cross it in some places and there it has been replaced by a wire fence which runs in some cases a few yards above and in some cases a few yards below the ruins of the wall, with the result that the sheep are now stopped by the wire fence where the wall is ruined and by the wall where it is intact, while formerly they were stopped by the wall all along.

The effect on the *Calluna* is most striking. Where the wire fence runs *below* the ruined wall the *Calluna* between it and the ruined wall is in a bad way and is nearly dead, while the *Calluna* on the lower side of the wire fence is perfectly healthy (see Fig. 1). Where the fence runs *above* the wall so that the area between the fence and the wall which was previously exposed to

<sup>1</sup> In this connection it is interesting to note that one of the keepers on Newmarket Heath has subsequently informed the writer that there is a considerable amount of heather growing on "Long Hills" on Newmarket Heath, and that there was far more heather there 20 years ago than there is now. It is cut down badly by the mowing machine each year—unfortunately from its point of view before the seed is ripe. This keeper expressed the opinion that if it were not for this regular mowing there would be a great amount of heather on many portions of Newmarket Heath.

<sup>2</sup> See Tansley, "Early Stages of the Re-development of Woody Vegetation on Chalk Grass-land." This JOURNAL, 10, 1922, p. 173.



sheep is now protected from them, scattered *Calluna* plants a few inches high and about three or four years old are colonising the ground and growing amongst the grass (see Diagram). This instance is an exceedingly pretty confirmation of the thesis that the existence of *Calluna* heath or grass-heath often depends simply on the relative severity of biotic attack, and fits in well with the theory that *Calluna* heath may often be and have been a particular developmental phase in the degeneration transition of woodland to grassland under the stress of increasing biotic attack. (See Diagram of the Biotic Zonation of Breckland, Part III, Fig. 1. This JOURNAL, 5, 1917, p. 13.)

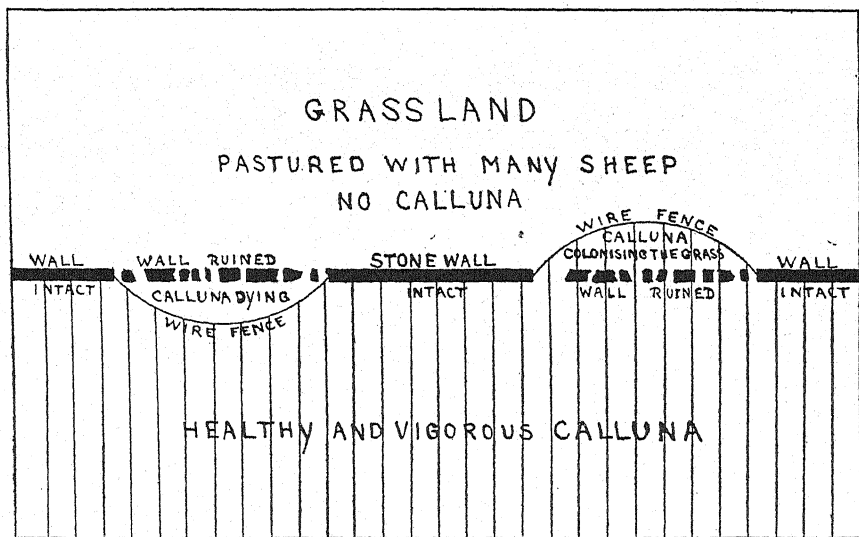


FIG. 1. Diagram illustrating the effect of sheep in limiting the distribution of *Calluna*.  
Moel Siabod in North Wales.

If the biotic attack was once low in intensity vegetation could decay on the surface and eventually produce surface layers of humus poor in lime which could become colonised by *Calluna* (cf. the gradual change from fen to moor formation consequent upon the production of surface layers of decaying humus poor in mineral salts).

The writer is inclined to believe that as the primitive woodland degenerated, largely owing to early pasturing, typical heath plants (*Calluna*, *Erica*, etc.) frequently colonised the remaining surface layers of decaying humus when the pasturing intensity was low and that thus woodland was often followed by broad zones of "heath." As the better heaths became more heavily pastured than the poorer ones and as the better soils became cultivated, the distribution of the *Calluna* and its associates became more and more restricted owing to the heavy pasturing and the cultivation, until the present distribution of *Calluna* in Britain on the poorer uncultivated soils not heavily pastured is probably merely a remnant of its former distribution. Exceptions to this

general process would occur where the former process of extension of the distribution of the heather at the expense of the primitive woodland is still going on at the present day on the poorer only slightly pastured soils—such as where the oak-birch woodlands are degenerating to heathlands occupied by *Calluna*. In comparatively recent times in many parts of England what is now termed the “common” used to be termed the “heath.” The use of “common” lands for *grazing* purposes is interesting in this connection. The writer has grown *Calluna* luxuriantly on fairly rich alluvial soil.

It is unsafe to infer (as is often done) from the fact that heather in England is typically associated with very poor soil that therefore heather prefers or flourishes best or would naturally survive best on very poor soils. *Calluna* can probably grow better on soils considerably richer than those with which it is commonly associated at the present time, but it has been exterminated on the better soils owing to heavier grazing and clearing in order to cultivate the better soils.

The survival of *Calluna* only on the patches of better soil in the same pasturing enclosure (i.e. with the same pasturing intensity), while on the poorer surrounding soil it has been exterminated by the given intensity of the biotic attack and has degenerated to dwarf grass, has probably something to do with the explanation of the case of the apparently anomalous distribution of *Calluna* which has been described by Rayner and Jones<sup>1</sup>. If this be so the survival of the *Calluna* only on the patches of better soil is probably a particular instance of the important general phenomenon, of great biological interest, viz. that organisms withstand specific detrimental influences only when the other conditions are favourable and die when they are not (cf. the restriction of tree growth to the damper valleys by biotic attack on the seedlings, Part III. This JOURNAL, 5, 1917, p. 9). Thus the influence of biotic attack on limiting the distribution of *Calluna* must be considered in addition to the lime distribution.

It may be that *Calluna* heath is largely to be regarded as a transition stage in the degeneration of woodland to grassland on certain soils where the biotic attack is sufficiently heavy to bring about the degeneration of the woodland and prevent it from regenerating, but not sufficiently heavy to exterminate the *Calluna* or to bring about the degeneration of the *Calluna* heath to grass-heath.

Probably after the degeneration of the primitive woodland and before the days of heavy pasturing by large domesticated herds and before the days of extended cultivation the distribution of *Calluna* in England was far more extensive than it is at present. It is noteworthy that it still occurs in every one of the Watsonian vice-counties of Great Britain (*Lond. Cat.* Ed. 10, 1908).

<sup>1</sup> Rayner, M. C. and Jones, W. N., “Preliminary Observations on the Ecology of *Calluna vulgaris* on the Wiltshire and Berkshire Downs.” *New Phytologist*, 10, 1911.

## IX. VIEWS RELATING TO THE PROBABLE FORMER DISTRIBUTION OF WOODLAND ON THE BRECKLAND HEATHS AND ON HEATHS AND TREELESS AREAS OF OTHER PARTS OF ENGLAND.

As no traces of natural woodland have been found on the upper dry sandy areas of Breckland and as the low rainfall and sandy soil make this district the climatically and edaphically driest in England, it had previously been thought doubtful if these areas ever bore natural woodland, and it was supposed that the dry sandy heaths of this district might quite possibly represent primitive heathland which had never been colonised by trees<sup>1</sup>.

On this account it was thought interesting to try to find out whether these dry Breckland sandy tracts are really probably primitively treeless. Information relating to this would be likely to have a bearing upon the probable former distribution of woodland in other parts of England. Considerable attention has therefore been devoted to obtaining information on this matter.

These Breckland heaths are the nearest approach in England to the North German heaths which have been described by Graebner<sup>2</sup>. The North German heath-area differs from the south-east European steppe region in possessing a damper climate not so intensely cold in the winter months and cooler in the summer without long continued dry periods. "The great heath formation of north-west Europe is typically developed on relatively poor sandy and gravelly soils whose climate is wetter than that which gives rise to steppe. The steppe climate is too dry for tree growth apart from local edaphic conditions but the heath formation exists side by side with woods, and in many cases has arisen as the result of the degeneration of woodland<sup>3</sup>." However, as stated above, it seemed that the dry sandy tracts of Breckland might very likely represent primitive heathland which had never been colonised by trees.

The profusion of flint implements of a great variety of different periods and their relative absence from surrounding districts indicates that Breckland was especially favourable as a habitat for prehistoric man, and it seems very probable that this may have been owing to its being dry, treeless or only thinly wooded and easily cleared of trees in primitive times, whilst adjacent districts were covered by dense impassable forest with thick undergrowth frequented by and capable of sheltering predatory animals.

The ancient linear defensive earthworks which occur in Breckland and to the southwestward, viz. the Black Ditches, Devil's Dyke, Fleam Dyke, Bran or Heydon Dyke, etc., run from the fenlands near the river valleys across the Chalk escarpment up to the Boulder Clay, which was once occupied by forest. The fosse or ditch of these dykes is typically on the western side.

<sup>1</sup> Tansley, A. G., *Types of British Vegetation*, p. 107.

<sup>2</sup> Graebner, P., *Die Heide Norddeutschlands*, Leipzig, 1901.

<sup>3</sup> *Types of British Vegetation*, p. 98.

In all probability these dykes were arranged across what was open treeless country at the time of their construction in order to prevent enemy tribes from invading the country of the eastern tribes from the west and driving away their domesticated herds of cattle across the open space.

Thus the areas crossed by these ancient defensive earthworks were probably open and treeless or at most very thinly wooded at the time of construction of the earthworks, and if the date of construction of these earthworks was known, it might be safely inferred that the areas were treeless or only thinly wooded at that date, and that if they were ever previously covered by a fairly thick tree community, most of the trees had disappeared or been destroyed before that time. Unfortunately, however, very little is known about the age of these dykes<sup>1, 2</sup>, except that Fleam Dyke is partly at least post-Roman. The most recent discussion<sup>2</sup> concludes that some at least are probably pre-Roman, and that the early Iron Age is a likely date for the Black Ditches (the only dykes of this series in Breckland proper), and for the Devil's Dyke, which crosses the chalk.

Most of Breckland was undoubtedly treeless during comparatively recent times until about the middle of the eighteenth century, when *Pinus sylvestris* was introduced into the district and various pine plantations were made on the open heaths<sup>3</sup>.

These pine plantations were often called by such names as "Folly Wood," so—if one may judge from place-names—it may be considered that the inhabitants imagined that the venture of making pine plantations in the otherwise treeless Breckland was a foolish act and would prove a failure.

At the present time these pine plantations are fairly flourishing and the trees, judged from their size, appear to be about 50 years old. As a matter of fact in many cases they are more than twice that age. Thus the trees only grow very slowly and in all probability this is chiefly due to the very poor water supply.

In addition to the pine plantations, various artificial plantations of *Quercus sessiliflora* and *Betula alba* sometimes occur on the upper sandy tracts. The trees in these deciduous plantations are not well grown, but nevertheless they can and do grow to a certain size. It must however be remembered that in the artificial plantations the young trees may have been protected from the competition of the heather for the limited water supply.

Occasionally bushes of *Crataegus monogyna* occur amongst the heather, but in these cases the branches are sometimes stag-headed and the trees are usually definitely limited in size. This applies for instance to an isolated specimen of *Crataegus monogyna* known as "Mile Bush" on Cavenham Heath.

<sup>1</sup> Hughes, T. McKenny, "The Cambridgeshire Dykes." *Journal of the British Archaeological Association*, 19, 1913.

<sup>2</sup> Fox, C., *The Archaeology of the Cambridge Region*. Camb. Univ. Press, 1923.

<sup>3</sup> Clark, W. C., "Some Breckland Characteristics." *Trans. Norfolk and Norwich Naturalists Society*, 8.

According to information received from an old shepherd, this bush is over 100 years old and has remained of a constant size for the past 60 years.

Sometimes seedling pine trees and young oaks occur amongst the thick heather and seem to be able to compete successfully with the heather, for they do grow, although slowly. On the upper drier areas however, when exposed to rabbit attack, they are always killed off by the rabbits before they can reach a sufficient size to become relatively immune. When rabbits are present in large numbers young seedling pines, oaks and birches can only colonise the valleys and lower portions of the valley sides<sup>1</sup>, probably chiefly because only in these damper positions can they produce tissue sufficiently quickly to overcome the damage caused by the rabbit attack. It has already been stated that numerous young pine trees are colonising and growing amongst thick heather inside a large rabbit-proof enclosure on the dry upper portions of Cavenham Heath near the Icklingham Road, although no young pines survive on the upper portions of the heath outside the rabbit-proof enclosure.

The area marked 15 on the map of Cavenham Heath<sup>2</sup> was once cultivated and protected by a rabbit-proof fence according to information received in Cavenham, and when the cultivation ceased it quickly regenerated *Calluna* heath. It was protected from rabbit attack for a time and the heather quickly became colonised by young pines. At that time some sheep also used to have access to the general area of the heath, and when the protecting fence round this area was eventually removed, the young seedling pine trees which had colonised it were quickly killed by the attacks of the sheep (and also probably by the rabbits)<sup>3</sup>.

It is thus seen that the rabbit attack and the previous sheep attack limits tree growth to the valleys and prevents the upper dry sandy areas of the heaths from being colonised by young trees and from being ultimately converted into woodlands.

Various observations indicate that a kind of plant which can grow up above another kind of plant has thereby a very great advantage in competition with the more dwarf vegetation and will under ordinary conditions dominate the latter, but that on the other hand the taller plants tend to suffer more from, and may be exterminated by, biotic attack.

From all these facts it appears that although the conditions in Breckland are the climatically and edaphically driest in England, *Pinus*, *Quercus*, and *Betula* seedlings can colonise and grow in thick heather when protected from rabbit and sheep attack and also in plantations. The ultimate "natural" highest type of vegetation on these sandy Breckland tracts under the present climatic conditions and in the absence of such animals as rabbits and sheep would thus probably be a pine or oak-birch woodland, but the presence of

<sup>1</sup> "General Effect of Rabbits on Vegetation." This JOURNAL, 5, 1917, p. 9.    <sup>2</sup> *Ibid*, 3, p. 217.

<sup>3</sup> It may be noted that the effect of rabbits on young trees is apt to be especially bad when the ground is covered with snow to such a depth that little but the stems of the young trees project above the snow mantle and are thus the chief kind of vegetation accessible to the rabbits.

rabbits and the previous presence of sheep have kept down the taller growing trees which would otherwise cover the area, and have allowed the shorter growing heather to survive.

Rabbits have only been introduced into England in comparatively modern times and their natural enemies have only been systematically kept down very recently. In Palaeolithic times domesticated herds do not seem to have existed and other grazing animals were probably kept down to relatively small numbers owing to the various predatory animals which existed at these periods. Breckland was undoubtedly partly surrounded by forests which could also supply tree seeds and thus it appears that during any periods in Palaeolithic times in which the climatic conditions resembled, or were damper than, the existing ones, Breckland was probably occupied by woodland provided that grazing animals were not numerous and provided that Palaeolithic man did not destroy all the trees. If the grazing intensity was very low and tree felling scarcely existent, it might even have been occupied by woodland during any Palaeolithic periods in which the climatic conditions were somewhat drier than they are at present. These remarks would also apply under these conditions during various periods in the Neolithic epoch, but during the later periods anyhow, and very likely during the early periods as well, tree felling by man was extensive, and man was fairly well equipped for dealing with predatory animals. Herds of domesticated animals also existed during these later periods, whereas there is no evidence that domesticated animals protected from their natural enemies existed in Palaeolithic times, during which period grazing animals were probably comparatively scarce.

It thus seems that when the grazing intensity was low and tree felling not extensive, Breckland was probably wooded, but that when tree felling was extensive and herds of domesticated cattle protected from their natural enemies existed, the probably former existing primitive woodland degenerated owing to felling of the old trees to clear the ground, and to provide wood for various purposes, and owing to the attack of the domesticated herds upon the tree seedlings in preventing them from growing and rejuvenating the woodland. It appears that the probable effect of prehistoric man and his herds in destroying the primitive woodland and killing the struggling young trees was continued later on into historic times by flocks of sheep pasturing on the heaths, and still later by the attack of rabbits after these latter had been introduced into England. Thus after any ancient woodland on this area had degenerated long ago owing to human occupation of the district and attack of domesticated herds, woodland never got a chance to regenerate and so an almost pure heath association was left behind from early Neolithic times until modern times when plantations protected from grazing were made on the heaths. It thus seems that if the biotic attack was slight, as it probably was, Breckland was probably wooded in early times.

As a matter of fact at the time of the Norman Conquest there was woodland

in various places on the N.E. corner of Breckland, and this woodland has since degenerated to heather. "There was woodland at various places in the eastern part of Breckland, Merton alone providing pannage for 240 hogs. During the next three or four centuries most of the local deeds contain reference to 'bruaria,' that is unproductive ground covered with heather and gorse<sup>1</sup>." These woodlands which existed in historic times were however on the extreme borders of Breckland<sup>2</sup>.

The young pine seedlings and the pines in the plantation seem to be able to grow better than the oaks and birches and this indicates that if *Pinus* was present in the district at any particular period during ancient times when the grazing was slight and when the climatic conditions resembled the existing ones it would probably have been able to compete successfully with any oak-birch woodland which might have existed, and would have been able to establish pine woods on these areas. *Pinus sylvestris* seems to have been abundant throughout Britain during part of the Neolithic epoch<sup>3</sup>, and if it had been present in Breckland during any particular period when the climatic conditions resembled the present ones any primitive woodland would probably chiefly be pinewood; but if *Pinus sylvestris* was absent from the district (as it seems to have been later on before it was reintroduced) any primitive woodland would probably consist chiefly of oaks and birches.

Various evidence seems to indicate that subsequently to the great Ice Ages, steppe periods may have intervened between periods of decreasing glaciation. If this be so, the gradual approach of steppe conditions might have helped in the degeneration of primitive woodland to an almost pure heath association. If any intervening steppe periods occurred during which the climatic conditions were much drier than those obtaining at present possibly these areas may have been too dry for tree growth even without grazing, and possibly any other vegetation may have been very sparse. These conditions would have facilitated the extensive blowing of sand which seems to have occurred in this district.

It has been considered that "natural causes of the degeneration of woodland and other associations are for the most part little understood<sup>4</sup>," but the explanation above given of the degeneration of probable primitive woodland in Breckland to a heath association owing to the attack of domesticated herds upon the seedlings in addition to the clearing by primitive man, and the prevention of the regeneration of the woodland in modern times owing

<sup>1</sup> Clarke, W. G., "Some Breckland Characteristics." *Trans. Norfolk and Norwich Naturalist's Society*, 8, p. 557.

<sup>2</sup> In passing it may be interesting to note that woodland on the edge of Breckland was the scene of the probably actual tragedy, which gave rise to the English version of the *Babes in the Wood* form of Fairy Tale. See Kent, Chas., *The Land of the Babes in the Wood*. Jarrold and Sons. (The house of the "Wicked Uncle" is still standing.)

<sup>3</sup> Reid, Clement, *The Origin of the British Flora*. Dulau & Co.

<sup>4</sup> *Types of British Vegetation*.

to the attack of rabbits, accords fairly well with the explanation given by Krause and Borgreve for the degeneration of oak woodland to *Calluna* heath in North Germany, and it is not in accordance with the theory of leaching of sandy soils given by Graebner for the same area.

In any case these Breckland sands have not been leached sufficiently by rain for tree growth to be unable to compete with the heather, for tree growth does as a matter of fact occur—in plantations and in enclosures where the young trees are protected from rabbits. The heather itself is usually thicker inside these enclosures and yet the young trees grow much better amongst thick heather when they are protected from rabbit attack than amongst thin heather where they are exposed to rabbit attack. This shows that the pines can compete satisfactorily with the heather and that leaching of the porous soil has not rendered the area incapable of becoming colonised by pines or brought about the degeneration of possible primitive woodland, but that this may have been brought about by biotic attack.

Graebner's theory of leaching is also in some other cases not satisfactory to account for the degeneration of woodland. In fact one would not expect leaching of the soil to counterbalance readily the great advantages which the tall *Pinus* would have over the dwarf heather, but grazing or rabbit attack can counterbalance this—in accord with the generalisation that taller growing plants are usually the ones which ultimately suffer most from increasing intensity of biotic attack. The point here is the *relative* effects of biotic attack of increasing intensities. A relatively slight intensity of biotic attack puts the trees at a great disadvantage compared with the dwarf heather, and ultimately when the biotic attack becomes much greater, as in various places in Breckland at the present time, it eventually leads to degeneration of the heather itself, which becomes replaced by *Carex arenaria* and ultimately by still more dwarf grass-heath.

Graebner attempts to prove the poverty of the soils occupied by heather relatively to the soils occupied by forest by data obtained from chemical analysis of the soil, especially from those made by Ramann. These results support the view that heaths occupy the poorer soils, but this fact is no proof whatever that the heath has come to occupy the soil owing to the soil being rendered poor by leaching. The occupation of the poor soils by the heather may be, and probably is, due to quite a different cause, viz. destruction by biotic attack of its taller competitors which were formerly smothering it, a destruction which would not occur so easily on the better soils with the same intensity of attack.

Graebner's theory of woodland degenerating to heath owing to leaching of the sandy soil may indeed be largely the opposite of the truth, i.e. an effect instead of a cause, i.e. the poverty and leaching of the sandy soil may be largely a result of the degeneration of forest to heather by the attack of pastured herds and rabbits, thus exposing the soil to the direct leaching



effect of rain, instead of the degeneration of the forest being due to leaching of the sandy soil. When the forest is degenerating owing to these other causes *Calluna* is able to invade its degenerating edge, and later on when the trees have disappeared the water which would otherwise be absorbed by the tree roots may soak through. But in the case of Cavenham Heath and other Breckland Heaths this has apparently not leached the soil sufficiently to prevent the tall growing trees from having a great advantage over the relatively dwarf heather and regenerating the forest when once the biotic attack is again removed, as inside enclosures.

It is apparently very dangerous to make deductions from soil analysis alone, as the particular differences in the soils may often largely be due to the presence or absence of particular plants instead of the absence of particular plants being due to particular differences in the soils.

It has already been mentioned that the fact that *Calluna* heath degenerates sharply at its edges when the degeneration is caused by biotic attack due to animals requiring extra food is suggestive, since forests and various other associations also chiefly degenerate at their edges.

It is sometimes stated that when the whole of the ground vegetation is of the heather type in degenerating woodland, it is doubtful if the young trees can grow<sup>1</sup>—though it is not implied that this is necessarily due to the heather itself. But the growing of young trees amongst thick heather in rabbit-proof enclosures on Cavenham Heath and their inability to grow amongst thinner heather when exposed to rabbits indicate that for Cavenham Heath this inability of the young trees to grow is not due to the whole of the ground vegetation being of the heather type but to the rabbits or other grazing animals which have probably originally brought about the degeneration of possible primitive forest killing off the young trees very rapidly indeed.

It is probably incorrect to speak of the taller woodland "giving way" owing to invasion by heath plants, as is often done. The woodland may "give way," but this is not owing to invasion by the lower growing heath plants. The invasion of the woodland by the heath plants is due to the "giving way" of the woodland owing to biotic attack on the seedlings.

The surface layer of dry peat and other things may render the young trees more readily killed by the rabbit attack, but in the case of Cavenham Heath and other Breckland Heaths rabbit attack is undoubtedly the immediate and effective factor in the matter and if it were not for this the *Calluna* heaths would regenerate to woodland.

The degeneration of woodlands to heather wastes of little value has been a serious economic problem in Germany and it appears probable that the practically valueless heather wastes of Breckland might be converted into useful pinewoods and perhaps dry oakwoods if the numbers of the rabbits were reduced and grazing on the open heaths was avoided. The grazing is

<sup>1</sup> *Types of British Vegetation*, p. 100.

not very profitable since the land is so poor and animals do not like the heather. The most important things which they eat are probably the young seedling trees which would otherwise gradually colonise these areas and change them into useful woodlands, and the afforestation of the heather wastes of Breckland would provide a certain amount of useful employment.

The slight humus and iron pans which have already been described as occurring in these heathland soils are certainly not sufficiently formidable seriously to hamper the growth of trees, and if these areas were afforested, there would be no need to break up these slight pans.

BEARING OF THE ABOVE FACTS ON THE PROBABLE FORMER DISTRIBUTION  
OF WOODLAND IN OTHER PARTS OF ENGLAND.

Very little semi-natural woodland is associated with the heaths of the London basin and it seemed possible that the heath formation originally colonised this and many other areas of the poorer English sands such as the Pliocene Crag, and in the south possibly also the Eocene Bagshot sands, and that these sands, or at any rate parts of them, had never borne natural woodland<sup>1</sup>.

The writer has, however, observed young seedling trees colonising the upper portions of the Eocene Bagshot sands and many other areas of English heaths and this phenomenon indicates that these sands can support tree growth and that they are not too dry or poor for this, and also that any original degeneration of primitive woodland on them has not been brought about by the soil becoming leached so much that it has become too poor for the trees to compete satisfactorily with the heather. It seems probable that any original degeneration was brought about by grazing and clearing and that biotic attack (under the already unfavourable conditions) has kept them comparatively free from the surrounding tree growth ever since, as in the case of the Breckland heaths.

In some cases such as the heaths of the London basin it seemed impossible to decide whether the heaths were primitive or derived from woodland—in other words to draw the limit between possibly primitive heaths and heaths which had undoubtedly been derived from woodland, for the two possible cases might be represented at the present time by identical plant associations<sup>2</sup>.

Since however it appears that the dry and poor sandy heaths of Breckland, which are climatically and edaphically the driest in England, can support trees provided that the seedlings are protected from biotic attack, and were probably wooded in pre-neolithic times when grazing animals were probably relatively scarce before the existence of domesticated herds protected from their various natural enemies, the apparently difficult problem of deciding

<sup>1</sup> *Types of British Vegetation*, p. 99.

<sup>2</sup> *Ibid.* p. 10.

whether any particular English heath was primitive or derived from woodland may have been indirectly solved. It seems that if grazing animals were once relatively scarce all the other English heaths probably once supported woodland and that probably none of them are primitively treeless.

It has also been considered that much of the area of the chalk downs has possibly never been covered by woodland. "There is good reason to suppose, as we have already pointed out, that much of the chalk pasture is extremely old and much of its area has possibly never been occupied by a tree association—perhaps because of an inadequate supply of underground water. The chalk grassland, which forms a very excellent light crisp pasture, has from time immemorial supported considerable flocks of sheep.

"The smooth curves of the chalk downs are occasionally broken by ancient trackways, camps and other earthworks of many periods from the Neolithic onwards. It has been suggested that the original purpose of many of these works was to shelter and defend the flocks from the attacks of predatory animals such as wolves coming from the forests of the lower country. Be that as it may, it seems unlikely that primitive man was responsible for the deforestation of such great areas of the chalk upland as are marked by traces of his presence and the conclusion is therefore indicated that much of this grassland is primitive, or at least has existed since the conditions of climate resembled at all closely those at present obtaining. There may well have been originally more scrub than there is now<sup>1</sup>."

The fact that the young trees degenerate so rapidly and readily from biotic attack on the upper dry sandy areas of Breckland where the conditions are already very unfavourable for them, whereas they do not degenerate nearly so readily from this influence and often manage to survive down the valley sides where the conditions are more favourable, is very interesting in this connection, for on the above mentioned areas of the chalk downs the conditions are probably also relatively unfavourable for tree growth. Thus the young trees on these areas of the chalk downs might degenerate very rapidly and readily from biotic attack by grazing animals compared with the rapidity of biotic degeneration under more favourable conditions. It thus seems that the above-mentioned vast tracts of chalk pasture on the downs may quite well have degenerated from primitive woodland owing to grazing especially if the Neolithic epoch was one of very vast duration as other evidences tend to indicate was in all probability the case.

The fact that the grass vegetation on the chalk downs grows considerably more luxuriantly than that on the Breckland heaths when both are protected from rabbits, probably indicates that there is a greater supply of underground water on the chalk downs than on the porous sandy tracts of Breckland, and yet even the latter would become colonised by trees if it were not for biotic

<sup>1</sup> *Types of British Vegetation*, p. 173.

attack on the tree seedlings, or if the biotic attack on the seedlings was low in intensity<sup>1</sup>.

The very rapid degeneration of seedling trees through biotic attack under the other unfavourable conditions in Breckland is also interesting in view of the fact that the conditions above the present altitudinal forest limit are also relatively unfavourable to growth, and it may well be that the extent of the depression of the altitudinal forest limit by the grazing of animals pastured above the tree zone may have been very considerably greater than might otherwise have been thought to be the case.

From observation in Breckland it appears that, if grazing animals were once relatively few before the existence of domesticated herds protected from their natural enemies, the primitive distribution of woodland in England under the existing climatic conditions was probably considerably more complete than has sometimes been supposed and that probably all the heaths of England<sup>2</sup> along with various other areas now treeless once bore woodland.

#### X. CONCLUDING REMARKS UPON BRECKLAND AND UPON ECOLOGICAL RESEARCH IN GENERAL.

ONE thing which clearly emerges from the work recorded in the foregoing pages is the great importance which must be attached to the biotic factors of the environment. Ecological factors are sometimes grouped solely as edaphic and climatic, but the highly important biotic factors should probably always be included in the classification. Apparently the presence of rabbits alone is sufficient to change the potentially dominant plant on Cavenham Heath from *Pinus sylvestris* to *Pteris aquilina* through a large number of various stages. This is clearly a profound change. The passing of England from a forest period into a grassland period may of late have been accelerated by the influence of rabbits.

While producing great changes in the ultimately dominant types of vegetation, the differential effects of particular intensities of rabbit attack upon the various types of vegetation produce great movements in the respective distributions of the different vegetation-units even when regarded over comparatively short periods of time. In fact one of the chief characteristics of the vegetation of Cavenham Heath is the extreme mobility of the various types owing chiefly to the differential influence of rabbits upon them.

<sup>1</sup> Mr Tansley has pointed out to the writer the possibility that the human and grazing factors preventing tree growth may quite conceivably have become operative before the general invasion by trees of the poorer and drier soils, such as those of Breckland and parts of the chalk downs, was completed; and this is the more likely if dry continental conditions intervened between the final retreat of the ice and the prevalence of climatic conditions like those now obtaining. If this were so we cannot altogether exclude the hypothesis of primitive treelessness of some areas, although the writer thinks that the presence of trackways, implements and other signs of early human habitation of such areas may quite well mean that man was also responsible for the disforestation of these areas.

<sup>2</sup> Except perhaps those on coasts exposed to violent winds.

The vegetation of Blakeney Point is also considerably more mobile than might have been suspected<sup>1</sup>. Doubtless the alterations in the vegetation due to topographical changes are far more rapid at Blakeney Point than on Cavenham Heath, owing to the presence of mobile shingle banks and sand-dunes in the former case; but, on the other hand, the general changes in the vegetation are far more rapid on Cavenham Heath than on Blakeney Point owing to the greater operation of biotic factors on Cavenham Heath, which completely outweighs in this respect the comparative absence of topographical changes. Breckland is a very suitable district in which to realise the great effects of animals upon plant life—owing to its uncultivated nature, the variety of its vegetation and the increasing severity of the grazing influences. Although the chief results are probably capable of very general application, the writer is sceptical as to whether there are many other districts in England which show such an extensive and beautiful generalised degeneration and zonation round the rabbit burrows, passing through so many stages as dealt with in Part III<sup>2</sup>.

Ecological research is concerned with living things, as they exist and change and interact in the living world, and it is an extremely interesting and fascinating study. One of its merits is that it gives the mind some faint conception of the complexity of nature. The problems awaiting solution are innumerable and many of them are extremely difficult to attack successfully. "The chief obstacle to the rapid development of ecology on fundamental lines is the laborious and time consuming nature of the work<sup>3</sup>."

Owing to the difficulty and complexity of the problems involved, it is advisable to choose the definite field problems which are to be taken up with very great care as otherwise much time may be wasted in futile attacks delivered along wrong lines.

It is probably much better in most cases to attack the easier problems or positions first, in the hope that these may throw some light upon or command the more difficult problems and positions and, as it were, outflank them. This is probably a better method and will ultimately advance the whole of ecology more than the method of devoting all the energy simply to a frontal attack upon some individual problem. It is probably advisable to devote much attention to the strategy and tactics of the attacks before delivering them with energy. This method of working will probably give far more results than a series of attacks delivered without careful arrangement. It is probably advisable to follow the Baconian method in the earlier stages of a research and to observe and collect a large amount of data relating to various phenomena before spending a lot of mental energy in trying to invent hypotheses to explain the various problems. While one is collecting preliminary data many of the problems in one's mind resolve themselves and the data themselves almost automatically suggest to the mind likely hypotheses to explain

<sup>1</sup> Oliver, F. W., "Blakeney Point in 1914." *Report of the Local Committee of Management, National Trust.*

<sup>2</sup> This JOURNAL, 5, No. 1, pp. 10-16.

<sup>3</sup> Tansley, A. G., *Types of British Vegetation*, p. xi.

the more difficult, and as yet unsolved, problems. Various experiments should then be carefully devised to try to test the various theories. Experimental methods used upon the facts of nature mark a great advance in checking and confirming the results of observation and inference and in giving fresh reliable results and sources of fresh data. Experiments tend to give definite results whereas soil analyses, for example, used alone in conjunction with possibly erroneous deduction are apt to give results which may very likely be the opposite of truth, for instance the "effect" instead of the "cause."

Instead of attempting to deal with ecological problems in the laboratory where very many factors are varied from their natural values, so that they are liable to alter or modify the result of the experiment unknown to the experimentalist, it is probably much better to take experimental methods to the plant in its home. Ecology means the study of organisms in their homes and the various theories relating to the actual ecological problems should be tested by experiments in the field itself, only altering one test factor at a time, and thus getting results definitely related to the effect of that factor upon the organisms, all the other factors remaining at their natural values.

Some of the problems which now badly need solution are those relating to competition between plants. Very little is known about this at the present time, and the solution of some problems relating to competition would be very valuable as being likely to throw important light upon many problems. At the present time the term "competition" is frequently used to cover any phenomenon which is not understood, and if more were known about competition, important light would probably be thrown upon many phenomena which are at present mysterious.

The observation of the great differential effects which the ravages of rabbits exert upon competing types of vegetation is possibly an advance in the right direction and may illustrate possible effects of the ravages of war upon human societies, but an enormous amount of work remains to be done, and should be done, upon phenomena associated with competition.

The effects of biotic influences by man and grazing animals upon the vegetation of England have probably been far greater and more extensive than is commonly or frequently realised—for instance, if it were not for these influences large areas of England including the whole of Breckland, the whole of the North and South Downs, and a considerable zone above the present tree limit (where there is sufficient foothold for tree growth) would probably be covered by trees. Thus, when anybody is working at the ecology of any ordinary non-wooded, non-coastal, and non-aquatic portion of England, it is probably advisable for him to realise very clearly that it was perhaps once covered by trees and perhaps would be at the present day if it were not for these biotic influences. This attitude would probably tend to make the student chiefly interested in the dynamic aspects of the vegetation and in its changes during various periods of time rather than in merely describing its static aspect at any given moment.

# THE ECOLOGICAL DISTRIBUTION OF ADULT CRANE-FLIES IN CARNARVONSHIRE

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(*With one Figure in the Text.*)

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## GEOGRAPHICAL FEATURES.

THE county of Carnarvonshire, N. Wales, has a very great surface variety, unequalled by any other county in the British Isles. Its greatest length is 55 miles from east to west, but from north to south it is 25 miles in the extreme east, narrowing down to 20 miles in a line from Bangor to Portmadoc, and ending in the snout-like projection of Braich-y-pwll, and the island of Bardsey in the west. The total area, excluding water, is 362,203 acres, including water 365,986 acres.

Looking at the sketch-map of Carnarvonshire (Fig. 1), one is at once struck by the fact that the county falls into two great divisions, an eastern and a western one; the east containing the mountains of Snowdonia, with the rugged passes and mountain torrents, while the west is a comparatively flat pastoral area. Furthermore the sea surrounds Carnarvonshire on the north, south, and west, while the two rivers, Conway and Glaslyn, form the greater part of its eastern boundary.

The county may further be divided into four zones: the sea coast, the region of farms, the wooded slopes and the rugged mountain area or mountain complex. There are 117 miles of sea coast, sometimes bordered by cliffs, but more frequently by marsh land and sand flats. If the upper limit of the second zone (the region of farms) be fixed at 500 feet (152 m.) above sea-level, it has been estimated that about 250 square miles is the content of the farm

zone. The slopes extending from 500 feet to nearly 1500 feet (456 m.) bear woods in some places, although these have now largely disappeared, especially the pine-woods, which were mostly destroyed during the late war to provide trench props. These woods are now being replanted. This area, now largely supporting the sheep grazing and slate industries, contains about 220 square miles. Finally, there are about 70 square miles of rugged mountain above 1500 feet reaching up to 3500 feet (1066 m.) at the summit of Snowdon; sheep also find pasture in this area.

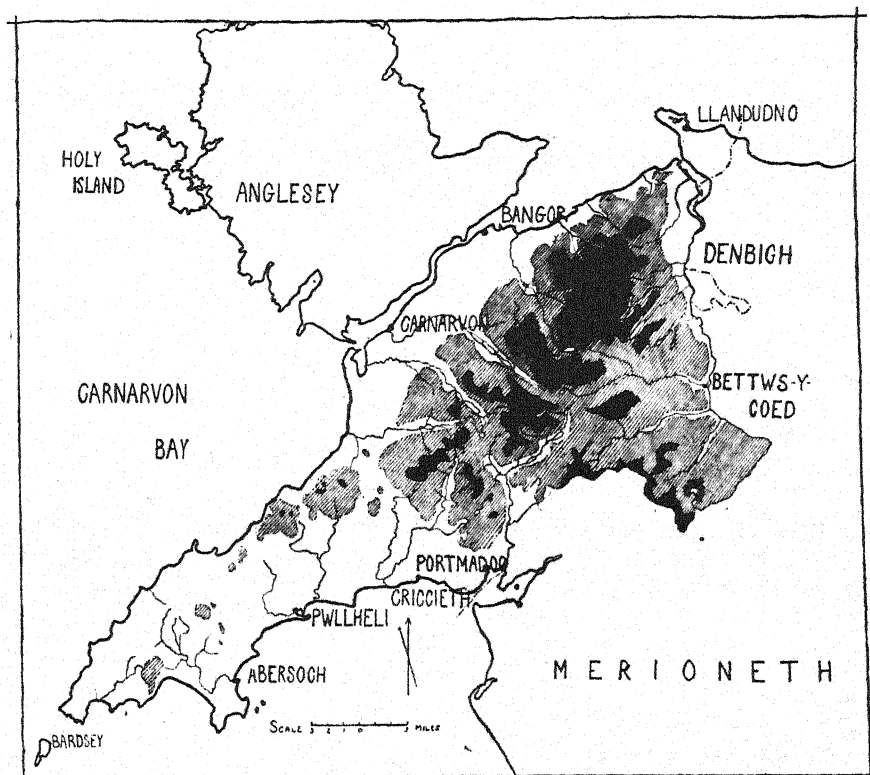


FIG. 1. Sketch map of Carnarvonshire. Coastlands and Region of Farms (0-500 feet) white, Hill slopes (500-1500 feet) diagonally shaded, Mountains above 1500 feet black.

The proportion of cultivation in the county is of interest. As has already been stated, the total acreage, excluding water, is 362,203 acres. Grassland, including rough grazing, is 277,528 acres, rotation grass and clover are 31,816 acres, and wheat, barley, oats, turnip, swedes, mangolds, and potatoes occupy 42,984 acres. In spite of the fact that there are many swamps, there are very few peat areas (3).

The wooded areas of the county (11,716 acres or 3.2 per cent. in 1909) are of two main types: the woods fringing the mountains and clothing the ravines



down which the mountain torrents rush, and the woods in the area known locally as the Lleyn, comparatively flat when compared with the mountain complex. Furthermore, there are numerous lakes, each of which sends one or more outflows down to the sea, and so there are innumerable mountain torrents and streams in the mountainous district, and streams which wind from place to place in the plain. The water surface acreage has been estimated at 3783 acres.

The rich crane-fly fauna depends mainly on the abundant water supply and on the wooded area (2).

#### HABITATS OF CRANE-FLIES.

In order to consider the ecological distribution of the crane-flies of Carnarvonshire, it has been deemed advantageous to propose 16 different habitats, and in all but one of these (sand dunes) the flies have been recorded and studied (see Table I). Many of these 16 habitats may occur in more than one of the four zones, and the habitats cannot in any way be considered as subdivisions of the zones.

It must be admitted that the habitats selected (Table I) are very vaguely defined and in all cases they could be subdivided into many more homogeneous, strictly defined habitats. The habitats employed were, however, carefully chosen to give as fair a representation of the ecological distribution of the adult flies as was practicable under the conditions of the work, and no such exact allocation of species to more numerous and strictly-defined habitats as could be made if the larvae were dealt with could be satisfactorily carried out.

The list in Table I is drawn up in alphabetical order for convenience. Since only about 1500 references are possessed by the writer, and about 100 species have been dealt with, these tables are to be considered as only rough preliminary indications of the ecological distribution of adult crane-flies. The references were all amassed by the writer between August, 1922, and December, 1923.

From a glance at Table I it will be seen that the most thickly inhabited habitat is the first, designated "Immediate neighbourhood of lakes, streams and rivers, on rocks, trees, bushes and grasses near by"; in this habitat 19 different genera are found, and 58 species. This represents a large proportion of the county crane-fly fauna, which consists of 26 genera and 99 species. The next most thickly populated habitat is "Hedgerows, ditches, and roadsides" (7), with 17 genera and 40 species; this is closely followed by (2), "Ravines with streams and woody elements," with 16 genera and 35 species. At the other end of the scale it will be seen that only 3 genera and 6 species inhabit (10) "Open mountain, (c) grassland" and (12) "Swampy situations, (b) woody swamps."

It should be noticed that the most thickly populated habitats are those in which there is a considerable amount of both shade and water. The presence of shade and water means that the humidity of the atmosphere in such a

TABLE I. *Alphabetical List of Carnarvonshire Crane-flies, showing the different habitats (1-16) in which they were found.*

1. Immediate neighbourhood of lakes, streams and rivers, on rocks, trees, bushes and grasses near by.
2. Ravines with streams and woody vegetation.
3. Mixed woods.
4. Coniferous woods.
5. Open fields, grassy banks of streams not in deep shade, and among bracken.
6. Rocky situations.
7. Hedgerows, ditches, and roadsides.
8. Open mountain, (a) bracken areas.
9. " " (b) bilberry and heather areas.
10. " " (c) grassland.
11. Swamps, (a) grassy.
12. " (b) woody.
13. Peat areas.
14. Sand dunes.
15. Gardens.
16. Houses, farm buildings, etc.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
<i>Acyphona maculata</i> ...	...	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Adelphomyia senilis</i> ...	...	.	x	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Antocha vitripennis</i> ...	...	x	.	x	.	.	.	.	.	.	.	.	.	.	.	.
<i>Cylindrotoma distinctissima</i> ...	...	.	.	x	.	.	.	.	.	.	.	.	.	.	.	.
<i>Dicranomyia aquosa</i> ...	...	.	x	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>autumnalis</i> ...	...	x	x	x	.	x	.	.	.	.	.	x	.	.	.	.
<i>chorea</i> ...	...	x	x	x	.	x	.	x	x	.	.	.	.	.	x	.
<i>didyma</i> ...	...	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>distendens</i> ...	...	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>dumetorum</i> ...	...	x	x	x	x	.	.	.	.	.	.	.	.	.	.	.
<i>lucida</i> ...	...	.	x	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>lutea</i> ...	...	x	x	.	.	x	.	x	.	.	.	.	.	.	.	.
<i>mitis</i> ...	...	x	x	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>modesta</i> ...	...	x	.	.	.	.	.	x	.	.	.	.	.	.	x	.
<i>morio</i> ...	...	.	.	.	.	.	.	x	.	.	.	.	.	.	.	.
<i>pilipennis</i> ...	...	.	x	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>stigmatica</i> ...	...	.	.	.	.	.	x	.	.	.	.	x	.	.	.	.
<i>Dicranota bimaculata</i> ...	...	.	x	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>pavida</i> ...	...	x	x	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Dolichopeza albipes</i> ...	...	x	x	x	x	.	.	x	.	.	.	.	.	.	.	.
<i>Empeda nubila</i> ...	...	.	.	.	.	.	.	x	.	.	.	.	.	.	x	.
<i>Erioptera flavescens</i> ...	...	.	.	.	.	.	.	.	.	.	x	.	.	.	.	.
<i>fuscipennis</i> ...	...	x	x	.	.	.	.	x	.	x	.	x	.	x	.	.
<i>macrophthalma</i> ...	...	.	x	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>taenionota</i> ...	...	x	x	x	.	.	.	x	.	.	x	.	.	.	x	.
<i>trivialis</i> ...	...	x	.	.	.	.	.	.	.	.	x	.	.	.	.	.
<i>Gonomyia conoviensis</i> ...	...	.	.	.	.	.	.	x	.	.	.	.	.	.	.	.
<i>dentata</i> ...	...	x	x	x	.	.	.	x	.	.	.	.	.	.	.	.
<i>lucidula</i> ...	...	x	.	x	.	.	.	.	.	.	.	.	.	.	.	.
<i>simplex</i> ...	...	.	x	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Idioptera apicata</i> ...	...	.	x	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>marmorata</i> ...	...	x	x	.	.	.	.	x	.	.	.	.	.	.	.	.
<i>Limnobia flavipes</i> ...	...	.	x	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>macrostigma</i> ...	...	.	.	x	.	.	.	.	.	.	.	.	.	.	.	.
<i>nigropunctata</i> ...	...	.	x	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>nubeculosa</i> ...	...	x	x	x	x	.	.	x	.	.	.	.	.	.	.	x
<i>quadrinotata</i> ...	...	.	.	.	x	.	.	.	.	.	.	.	.	.	.	.
<i>stigma</i> ...	...	.	.	x	.	.	.	x	.	.	.	.	.	.	.	.
<i>trivittata</i> ...	...	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Limnophila aperta</i> ...	...	.	x	.	.	.	.	.	x	.	.	.	.	.	.	.
<i>bicolor</i> ...	...	.	x	x	.	.	.	.	.	.	x	.	.	.	.	.
<i>lineola</i> ...	...	.	x	.	.	.	.	x	.	.	.	x	.	.	.	x
<i>lineolella</i> ...	...	.	x	x	x	.	.	.	.	.	.	.	.	.	.	.
<i>meigenii</i> ...	...	.	x	.	.	.	x	.	.	x	.	.	.	x	.	.

TABLE I—continued.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
<i>Limnophila nemoralis</i> ...	...	x	x	x	.	x	x	x	.	x	x	.	.	.	x	.
„ <i>ochracea</i> ...	...	x	x	x	x	.	x	.	.	.	.	.	.	.	.	.
„ <i>punctum</i> ...	...	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Lipsothrix errans</i> ...	...	.	x	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Molophilus biflatus</i> ...	...	.	.	.	.	.	x	x	.	.	.	.	.	.	.	.
„ <i>flavus</i> ...	...	x	x	.	.	.	.	.	.	.	.	.	.	.	.	.
„ <i>medius</i> ...	...	x	x	.	.	.	.	.	.	.	x	.	.	.	.	.
„ <i>occultus</i> ...	...	x	x	.	.	.	.	.	.	.	x	.	.	.	.	.
<i>Nephrotoma dorsalis</i> ...	...	x	.	.	x	.	.	.	.	x	x	.	.	.	.	.
<i>Osmosia albitibia</i> ...	...	x	.	x	.	.	x	x	.	.	.	.	.	.	.	.
„ <i>nodulosa</i> ...	...	x	x	x	.	.	x	x	.	.	.	.	.	.	x	.
<i>Pachyrrhina crocata</i> ...	...	.	.	x	.	.	.	.	.	.	.	.	.	.	.	.
„ <i>flavescens</i> ...	...	x	.	.	.	x	.	x	.	.	x	.	.	.	.	.
„ <i>imperialis</i> ...	...	x	x	x	x	x	.	x	.	.	.	.	.	.	x	.
„ <i>maculosa</i> ...	...	.	.	.	.	.	.	.	.	.	.	.	.	.	.	x
„ <i>quadrifaria</i> ...	...	x	.	.	.	.	.	x	.	.	.	.	.	.	.	.
<i>Pedicia rivosa</i> ...	...	x	.	.	.	.	.	.	.	.	x	.	x	.	.	.
<i>Pilaria discicollis</i> ...	...	.	.	.	.	.	.	x	.	.	.	.	x	.	.	.
<i>Pseudolimnophila lucorum</i> ...	...	.	.	.	.	.	.	.	.	.	x	.	.	.	.	.
„ <i>sepium</i> ...	...	.	.	.	.	.	.	.	.	.	x	.	.	.	.	.
<i>Rhipidia maculata</i> ...	...	x	.	x	.	.	.	x	.	.	.	.	.	.	x	x
<i>Rhypholophus haemorrhoidalis</i> ...	...	.	.	.	.	.	.	x	.	.	.	.	.	.	.	.
„ <i>varius</i> ...	...	x	.	x	.	.	.	.	.	.	.	x	.	.	.	.
<i>Symplectomorpha stitica</i> ...	...	.	x	.	.	.	.	x	.	.	.	.	.	.	.	.
<i>Tipula alpium</i> ...	...	x	.	x	.	x	x	.	.	x	.	.	.	.	.	x
„ <i>cava</i> ...	...	.	.	x	.	x	.	x	x	.	.	.	.	.	.	.
„ <i>diana</i> ...	...	.	.	.	.	.	.	.	.	.	.	.	x	.	.	.
„ <i>excisa</i> ...	...	.	.	.	.	.	.	.	x	.	.	.	.	.	.	.
„ <i>fascipennis</i> ...	...	x	x	.	.	x	.	x	.	.	.	.	.	.	.	.
„ <i>flavolineata</i> ...	...	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.
„ <i>gigantea</i> ...	...	x	.	.	.	.	.	x	.	.	.	.	.	.	.	x
„ <i>irrorata</i> ...	...	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.
„ <i>lateralis</i> ...	...	.	.	.	.	x	.	x	.	.	x	x	.	.	.	.
„ <i>luna</i> ...	...	.	.	.	.	.	.	.	.	.	x	.	.	.	.	.
„ <i>luteipennis</i> ...	...	.	.	.	.	.	.	.	.	x	.	.	.	.	.	.
„ <i>lutescens*</i> ...	...	14	4	7	1	3	.	12	2	.	1	4	1	.	.	1
„ <i>marmorata</i> ...	...	x	.	x	.	.	.	x	x	x	.	.	.	.	x	x
„ <i>montium</i> ...	...	.	.	.	.	.	.	.	.	.	x	.	.	.	.	.
„ <i>ochracea</i> ...	...	.	.	.	.	.	.	.	.	.	.	.	.	.	x	.
„ <i>pagana</i> ...	...	.	.	.	.	.	.	.	.	x	.	.	.	.	.	.
„ <i>paludosa</i> ...	...	x	x	x	x	x	x	x	x	x	x	x	x	.	x	x
„ <i>pelio stigma</i> ...	...	.	.	.	.	.	.	.	.	.	x	.	.	.	.	.
„ <i>pruinosa</i> ...	...	.	.	.	.	.	.	x	.	.	.	.	.	.	.	.
„ <i>rufina</i> ...	...	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.
„ <i>scripta</i> ...	...	x	x	x	x	x	x	x	x	x	.	x	.	.	.	x
„ <i>selene</i> ...	...	.	.	.	.	.	.	.	.	.	.	.	x	.	.	.
„ <i>unca</i> ...	...	x	.	x	.	.	.	x	x	.	x	x	.	.	.	.
„ <i>varicornis</i> ...	...	x	.	.	.	.	.	x	.	.	x	.	.	.	.	.
„ <i>vernalis</i> ...	...	.	.	.	.	.	.	.	x	.	.	.	.	.	.	.
<i>Tricyphona claripennis</i> ...	...	.	.	.	x	.	.	x	.	.	x	.	.	.	.	.
„ <i>immaculata</i> ...	...	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.
„ <i>littoralis</i> ...	...	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.
„ <i>lucidipennis</i> ...	...	.	x	.	.	.	.	.	.	.	.	.	.	.	.	.
„ <i>occulta</i> ...	...	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.
„ <i>schummeli</i> ...	...	.	.	.	.	x	.	.	.	.	x	.	.	.	.	.
Total species, 99	...	59	36	29	10	18	9	41	12	11	7	25	7	8	nil	9
Total genera, 26	...	19	16	13	7	6	6	17	5	4	3	9	3	5	nil	4

\* The numbers in this row represent the numbers of records of *Tipula lutescens* in each habitat.

TABLE II. *Number of Species and Genera of Crane-flies found in various numbers of Habitats.*

No. of habitats	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Totals
„ species	42	15	13	8	3	9	3	2	.	1	1	1	.	.	1	99 species
„ genera	5	5	2	2	3	2	1	2	1	.	1	.	1	.	1	26 genera

TABLE III. *Number of Species per Genus of Crane-flies in Carnarvonshire.*

12 genera contain	...	1 species each
5 „ „	...	2 „ „
2 „ „	...	4 „ „
2 „ „	...	5 „ „
1 genus contains	...	6 „ „
1 „ „	...	7 „ „
1 „ „	...	8 „ „
1 „ „	...	13 „ „
1 „ „	...	25 „ „
26 genera contain	...	99 species in all

situation is considerable compared with a situation exposed to the wind, or a situation with shade but without an abundant water supply, e.g. pine and fir woods.

The density of the population of species may be gathered from the totals at the foot of each column of Table I and this enables a rough judgment to be formed of the relative values of the different habitats as ecological factors.

#### RELATIVE HUMIDITY.

Relative humidity may be defined as the amount of water vapour the air contains compared with the amount it would contain if it were saturated with moisture from a flat surface of water at the same temperature. The relative humidity falls as the temperature rises. Relative humidity may therefore be said to depend upon the interaction of temperature with the supply of liquid water. The rate of evaporation is obviously important as it is clear that the more evaporation takes place, the more water vapour there will be in the atmosphere, at any rate for a short time. Evaporation depends mainly on (1) the vegetation, (2) the dryness of the wind, and (3) the heat of the sun.

It is on such factors as these that the ecological distribution of adult crane-flies largely depends. Of course the distribution of the immature forms is a great factor in the distribution of the adult flies and there was no opportunity of working out the distribution of the larvae, but it is believed that this will be found to correspond largely with that of the adults.

All the habitats which have a large crane-fly flora, such as (1), (2), (3), (7), (11), are characterised by a plentiful water supply and a large amount of shade. This means that the relative humidity in such places is often large, for even if the temperature does rise considerably there is a plentiful supply of fresh water to evaporate, e.g. the water of the streams, lakes, ditches, etc. There is usually a fair amount of moisture in mixed woods because there is usually enough undergrowth to prevent excessive evaporation.

The texture of the soil is an important factor in evaporation, as certain soils both allow the rain to sink in and have great capillarity, i.e. allow the moisture to rise to the surface readily. On the other hand, some soils do not permit the rain to sink in, and so most of it runs off the surface. Other soils permit the rain to sink in, but cannot draw it up again, e.g. sand. A clay soil is an example of a soil which does not allow the rain to sink in rapidly. The soil in a well-kept garden is a good example of a soil which allows the rain to sink in quickly and at the same time possesses good capillarity. Hence "Gardens" ranks among the most thickly-populated habitats. Not a single crane-fly has been recorded from the habitat designated "Sand dunes."

It will be seen that the more exposed the habitat is, the less dense is the crane-fly population, regardless of the amount of water available or on the other hand of the dryness of the position. Thus it is found that in such damp habitats as "Peat areas," "Grassy banks of streams not in deep shade," only 5 to 6 different genera are recorded and 8 to 18 species. Also in such habitats as "Open mountain" only 3 to 5 genera are recorded with a corresponding decrease in the number of species, 6 to 11. That other factors besides exposure affect the abundance of crane-flies is shown by the fact that in such habitats as "Coniferous woods" and "Swampy situations, (b) woody swamps" the crane-fly population consists of 3 to 7 genera and 7 to 10 species. This probably indicates that in the case of the pine and fir woods the lack of undergrowth and the resultant decrease in retention of moisture affects the presences of the adult flies. In the case of the woody swamps, the reason for the small numbers of flies, in spite of the dampness, may be some fault in compilation of the tables resulting from the narrow line separating this habitat from that designated "Immediate neighbourhood of streams, etc." and "mixed woods."

#### DISTRIBUTION OF INDIVIDUAL GENERA AND SPECIES.

Suppose one considers the ecological distribution of a large genus of crane-flies, e.g. *Tipula*, it is at once apparent that although representatives of the genus are found in 15 different habitats, only one of the species, i.e. *T. paludosa*, is found in all the 15 habitats, and it is only accidentally found in some of them. In the same way *T. scripta* and *T. lutescens* are found in 12 and 11 ecological habitats respectively.

The numbers opposite *T. lutescens* in Table I, representing a total of 50 records of this species, show that though this fly has a relatively powerful flight, it is most abundant in damp places, habitats (1), (2), (5), (11) and (12) giving 26 records, or more than 50 per cent. of the total number for the species. The fly is also recorded 12 times, or about 25 per cent., from "Hedge-rows, ditches, etc.," which are in most cases damp also. Therefore in roughly 75 per cent. of the recorded cases *T. lutescens* appears in damp and wet places in the neighbourhood of water. It occurs 7 times in "Mixed woods," which

are naturally shady and, owing to the cover, have a comparatively high relative humidity: very often streams run through them as well. The remaining ecological habitats in which *T. lutescens* occurs at all are dry ones, e.g. "Pine and fir woods," "Open mountain areas, (a) bracken and (b) grass"; however there are only five such appearances recorded, and this is explained by the power of flight of the insect, as anyone who has observed it flying can verify. In fact the writer believes that the marked sexual dimorphism exhibited in the coloration of the wings is connected with the strong flight, as it is in dragon-flies. In connection with the supposed protective mimicry exhibited by the female *T. lutescens*, it is interesting to note that Alexander (1) observes that "dragon-flies appear to be the most serious enemies of the active adults" of *Eriocera longicornis* Wlk. It will be seen that, although the fly is powerful enough to fly away from the haunts of its larvae, it is usually restricted to the neighbourhood of streams and damp places.

*T. marmorata* is found in seven different ecological habitats, but unlike *T. lutescens* it shows a preponderating occurrence in dry habitats, e.g. (7) "Open mountain, (b) heather and bilberry areas." This is most interesting, as the larvae are only found in *Hypnum* moss on rocks and stones and rotten tree trunks under trees, near streams, etc.

*T. scripta* is found about equally in such habitats as (2), (3), (4), (7), (8), (9) and (12), thus showing no particular restriction in ecological distribution.

As contrasted with these species of *Tipula* that show a wide ecological distribution, several species (13) are only recorded from one habitat. Though this is of course partly due to the small amount of data available, some species may be confined to single habitats.

The genus *Dicranomyia* is represented in 11 different ecological habitats. *D. chorea* occurs in eight habitats and *D. autumnalis* occurs in seven. On the other hand, six different species occur only in one habitat. *D. chorea* is found as to about 66 per cent. of occurrences in "Hedgerows, etc." and "Gardens," the remaining 33 per cent. in various habitats. *D. autumnalis* is found about 39 per cent. in "Hedgerows, etc.," about 25 per cent. in "Mixed woods," and in five other habitats, yet never more than 14 per cent. in any one other. *D. pilipennis*, on the other hand, is never found in any other habitat except "Ravines with streams, etc."; *D. didyma* is similarly found solely in the immediate neighbourhood of water (1).

*Pachyrrhina imperialis* is found in seven different ecological habitats, yet in 48 per cent. of the recorded cases it appears in "Mixed woods," and in 20 per cent. in "Ravines with streams, etc.," where there is always a considerable amount of shade. The remaining 32 per cent. of its occurrences are in "Open fields, etc.," the immediate neighbourhood of water, "Hedgerows, etc.," "Gardens," and "Pine and fir woods."

*Limnobia nubeculosa* is found in eight habitats, and occurs as to 46 per cent. in "Mixed woods" and "Ravines with streams, etc.," and another

26 per cent. in "Hedgerows, etc." The remaining 28 per cent. appear in the immediate neighbourhood of water, "Rocky situations," "Pine and fir woods," "Gardens" and "Houses, etc."

*Limnophila ochracea* is found in six different habitats; 43 per cent. in "Mixed woods," and 16 per cent. in each of the following habitats: "Ravines with streams," the immediate neighbourhood of water, and "Hedgerows, etc." It is also found in "Open fields, etc." and "Pine and fir woods."

*Limnophila nemoralis* occurs in ten different ecological habitats: 37 per cent. in the immediate neighbourhood of water, 21 per cent. in "Hedgerows, etc." and in seven other habitats less often.

*Erioptera taenionota* occurs in six habitats: 35 per cent. in the immediate neighbourhood of water, 31 per cent. in "Hedgerows, etc." and also in "Ravines with streams, etc.," "Mixed woods," "Swampy areas, (a) grassy" and "Gardens."

*Pedicia rivosa*, the only representative of the genus, occurs in three habitats, i.e. "Peat areas," "Swamp areas, (a) grassy," and the immediate neighbourhood of water. The larvae of this fly live in streams and swamps, and although the adult fly is large, it appears to remain in the habitats where its larvae have lived.

*Cylindrotoma distinctissima* is only found in "Mixed woods" and never anywhere else. This appears to be another case in which the range of the larvae and the adult fly are identical.

So far enough data have not been collected to deal with all the genera adequately, as the writer only possesses about 1500 records of about 100 species, amassed by himself, and there are no other records available. After further work it will be possible to allocate more exact ecological areas to the particular flies.

At present only a rough indication can be given, as shown in Table I, as to where the different flies have been found, and one must not be in too much of a hurry to draw conclusions. One elementary fact stands out however (Table II). Many more flies, both species (42 per cent.) and genera, are restricted to one ecological habitat; there are fewer occurring in two habitats (15 per cent. of the species), still fewer in three (13 per cent.), and only one species in 10, one in 11, one in 12 and one in 15 habitats. A similar rule holds for the number of species in each genus (Table III), e.g. 12 genera possess only 1 species, four possess 2, while only one possesses 6, one 7, one 8, one 13 and one 28 species. In several cases the distribution of the mature fly seems to correspond with that of the larvae.

#### OTHER METEOROLOGICAL FACTORS.

*Rainfall.* We have seen that relative humidity is probably the leading factor in determining the ecological distribution of crane-flies, though no direct comparisons of abundance of these insects with measured atmospheric

moisture have been made. It is, however, of interest to compare the temporal abundance of crane-flies with the occurrence of rainfall.

Such a comparison in the summer of 1923 points to the conclusion that a week of average, or just under the average, rainfall (about one inch or somewhat less in the week) following excessive rain is apparently the most favourable condition for the abundant occurrence of crane-flies on the wing. If there is a dry period, following one of less than the average rainfall, the number falls off, and the same effect is produced during a period of excessive rainfall, such as 2 to 3 inches a week. The optimum weekly rainfall for crane-flies under the conditions of Carnarvonshire appears to lie between 0.55 and 0.95 inch (say 13 to 23 mm.).

The individual genera show somewhat different relations to rainfall. Thus numbers of species of *Tipula*, large heavy insects, remain on the wing through relative drought, while heavy rainfall has a lasting effect in depressing the number of species of this genus. The rather fragile flies belonging to the genus *Dicranomyia* follow the general rule given above more closely, disappearing or practically disappearing in drought or excessive rain, and occurring in the greatest numbers in weeks showing 0.7 to 0.95 inch of rain. Most of the small flies of the genus *Erioptera* appeared in a wet week following drought, and least during drought, but the correlation with rainfall is not so close as in the other two genera mentioned. The occurrence of *Limnobia* in relation to rainfall resembles that of the closely allied *Dicranomyia*, while *Limnophila* showed the highest numbers during a week of relative drought and the next highest during two weeks of rather low rainfall (0.56 and 0.71 inch).

*Temperature.* There is also a correlation between temperature and the number of species of crane-flies on the wing, but the data are inadequate to any detailed discussion. Graham-Smith (4) concluded that temperature influenced the activities of flies more than any other meteorological condition, and also that there is a critical temperature below which they cannot emerge from the pupae. The writer believes however that, once the critical temperature is reached, the number of adult crane-flies depends more on rainfall, probably acting through relative humidity, than on temperature or any other factor. This deviation from Graham-Smith's conclusion probably depends on the fact that crane-flies usually produce but one, or sometimes two, broods a year, while the flies Graham-Smith worked with breed continuously throughout the fly season. Also his results are based on active flies caught in traps, while the writer's include adults at rest in hiding places as well as those actually flying.

*Wind.* Excepting its effect on relative humidity the chief influence of wind on crane-flies is to drive them into shelter where they are not easily found, and one must be on guard against concluding that there is any direct correlation between wind and number of adults occurring. No adequate data are available.



## ALTITUDINAL DISTRIBUTION.

So far as the rather scanty data available allow of a conclusion, one may say that the bulk of the species are lowland forms, and that above 1500 feet the crane-fly fauna is negligible. Flies have been recorded above this height, but it seems probable that their occurrence is only spasmodic and is occasionally caused by high winds. Only 20 species, belonging to eight genera, are recorded above 900 feet, and 12, belonging to five genera, from 1000 to 1500 feet. One species, *Dicranomyia didyma*, occurs only above 1200 feet and must therefore be considered a mountain form. *Tricyphona littoralis*, *Limnophila bicolor* and *Idioptera apicata* occur only above 500 feet and are therefore relatively upland forms. Some occur only below 500 feet, and a few only below 200, and are therefore distinctly lowland forms. Other species, on the contrary, show a wide range of altitude, *Dicranomyia autumnalis*, for instance, ranging from sea-level to 1000 feet. The majority depend almost entirely on the extent or range of their own ecological habitats. For instance, the flies characteristic of "mixed woods" occur in these whether they are at sea-level or at an altitude of 600 feet.

I should like to take this opportunity to express my thanks to Dr C. L. Walton, Adviser in Entomology in the North Wales district, for his never-ending encouragement and advice throughout the work, and also to Prof. R. G. White for his permission to use the Entomological Laboratory in the Department of Agriculture, Bangor.

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# THE INCIDENCE OF SPECIES IN RELATION TO SOIL REACTION<sup>1</sup>

By E. J. SALISBURY.

(*With ten Figures in the text.*)

It is not proposed to discuss here the origin and nature of the acids present in soils. That real acids are present has been demonstrated by the numerous researches which have shown that the hydrogen-ion concentration of the soil solution is often considerably in excess of that of pure water. The fact that, as shown by the writer, both for sand dunes and woodlands, for a given type of plant covering and on a uniform mineral substratum, the real acidity increases with the organic content, is strong presumptive evidence that the products of organic decomposition are mainly involved.

In some cases the acids may be siliceous or a consequence of hydrolysis of mineral salts, such as those of aluminium or iron. Acidity may also be an outcome of adsorption and base exchange. But from the point of view of the effect on vegetation of the hydrogen-ion concentration it is immaterial whether the real acidity is a direct or an indirect result of organic decomposition, and for the moment we need not discriminate between a direct or an indirect toxic action.

It is almost certain that the causes as well as the direct effects of soil acidity are various and much harm has probably been done to the progress of knowledge by the exclusive attitude adopted by the protagonists of the various views that have been put forward.

The chief interest for the ecologist is whether or not there is a marked relation between reaction and vegetation and the causes of the reaction, if varied, only become of biological importance if they lead to differing results.

It would seem almost superfluous to emphasise that soil reaction is only one of the many factors which appear to determine the nature of the plant covering. But the statements of some investigators would appear to warrant the assumption that the effect of other habitat factors in modifying the tolerance of species for high concentrations of hydrogen-ions has often been insufficiently recognised. The fact that for instance a given species is found growing in soils exhibiting a wide range of reaction has been taken as evidence that reaction has little influence on distribution. The argument would only be valid if the species occurred with equal frequency and in equal vigour throughout the range in question.

Acidity, like so many other habitat factors, can, under the protected conditions of cultivation, be tolerated to a degree which a species is not found to endure in nature. Because aquatics, such as *Butomus umbellatus* or

<sup>1</sup> Contribution to discussion on soil acidity at British Association Meeting, Liverpool, 1923.

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*Alisma plantago*, will grow and flower in ordinary garden soil, or *Statice binervosa* on stiff clay apparently even more vigorously than on its native shingle, no one would suggest that the former are not rightly regarded as aquatics or that the latter is not really a littoral plant, finding in these respective natural habitats the optimum conditions for establishment and maintenance under natural conditions of competition. Similarly because it may be possible to grow species in water cultures, or even in soils, of high acidity in the garden or experimental plot, we are not warranted in assuming that therefore soil reaction plays little or no part in determining the incidence of the particular species in nature.

Various workers have shown that in water cultures there is a tendency for selective absorption of roots to bring about an approach to the neutral condition, but the complex equilibrium system represented by the soil is strongly buffered, particularly when, as in many natural soils, large proportions of colloidal substances are present. Owing to this strongly buffered condition the reaction of a soil is comparatively stable despite the variations in the respiration of the root systems and the fluctuating character of the  $\text{CO}_2$  output from the teeming micro-flora and -fauna. Indeed, such seasonal changes as may occur in reaction appear to correspond rather to the effect of the summer drought on the colloidal fractions and their buffering action than to the spring and early autumn maxima in the organic life of the soil. We may assume for our present purpose that, within comparatively narrow limits, the reaction of an undisturbed soil is fairly constant throughout the year.

With the object of estimating the effect of reaction in the conditions of nature a few species were chosen of which samples had been collected from a large number of localities.

The locations had been chosen in the ordinary course of ecological investigation; the only bias in their selection is that extreme types of habitat tend to be sampled more frequently in proportion to the normal than their actual numerical frequency warrants, hence the mode tends to be less pronounced and the gradient of the curve less steep than in an ideal curve. For our present purpose when a large number of soil samples were taken close together in the same locality all those of identical  $\text{pH}$  value were treated as one determination. In this way any "overloading" due to an exceptional number of samples being taken in a particular type of locality is avoided.

The area covered by the samples extends from Cornwall and Kent in the south to Lancashire and Yorkshire in the north; most of the localities however were in Hertfordshire, Herefordshire, Shropshire, Cornwall, Somerset, Surrey and Kent.

The data are plotted as frequency curves with the  $\text{pH}$  values as abscissae and the number of localities as ordinates. It will be apparent that the curves approximate to normal variation curves with a fairly high degree of dispersion.

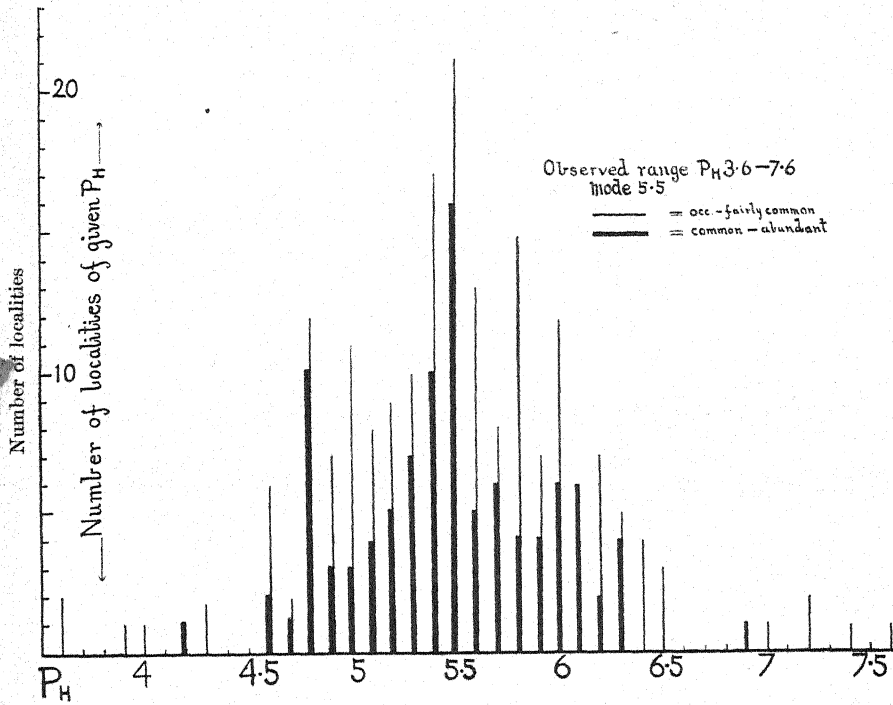


FIG. 1. Variation in the Hydrogen-ion concentration in 200 different localities for *Pteridium aquilinum*.

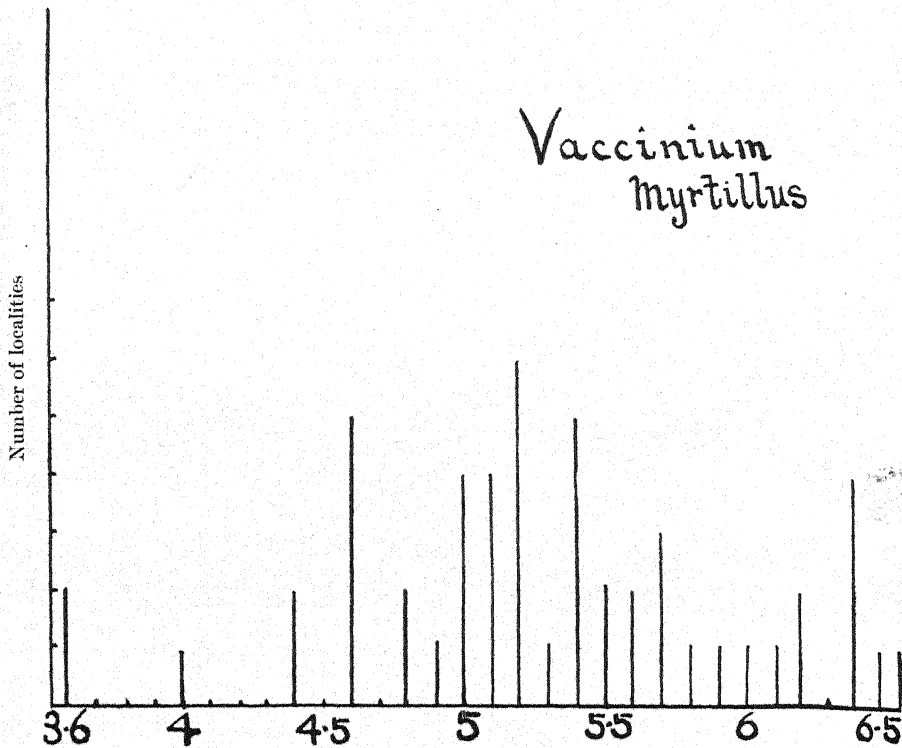


FIG. 2. Hydrogen-ion concentration in 52 localities for *Vaccinium myrtillus*.

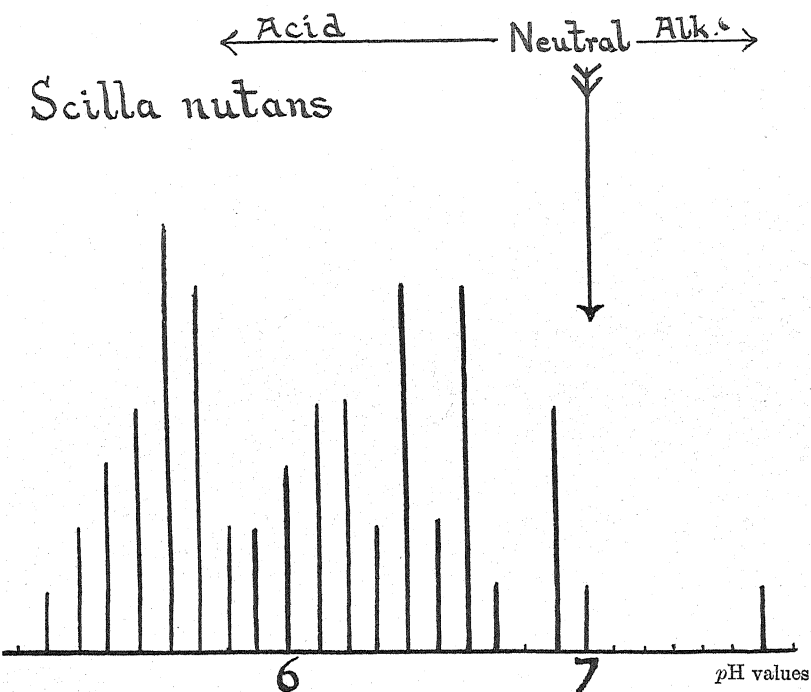


FIG. 3. Hydrogen-ion concentration in 60 localities for *Scilla nutans*.

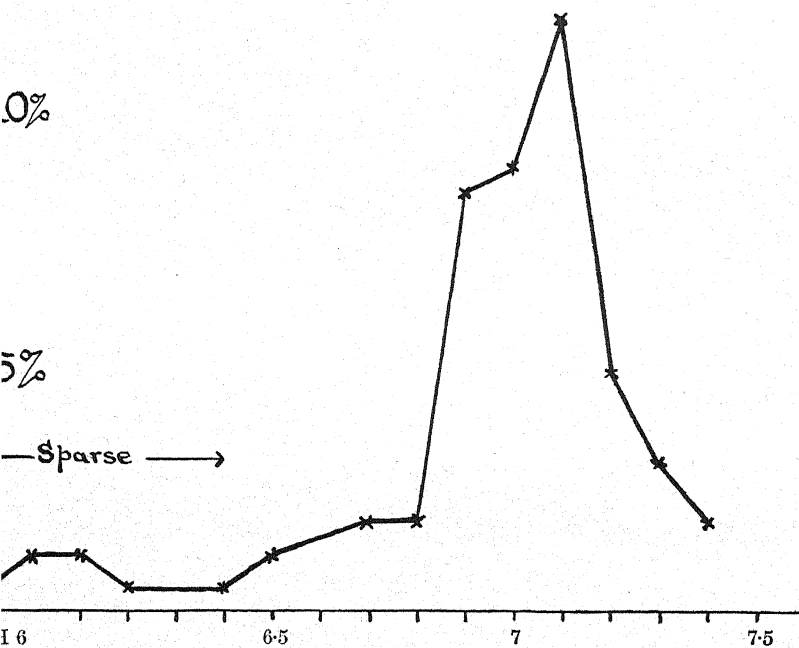


FIG. 4. *Psamma arenaria* at Blakeney Point.

It may be assumed that since very acid and very alkaline soils are of rare occurrence a random sampling of a large number of soils would yield a normal frequency curve representing the frequency distribution of soils of different reaction. If a species existed which was entirely indifferent to soil reaction it is evident that the distribution curve obtained by sampling all the soils on which it grew would be identical with that for the frequency distribution of soils of different reaction; in other words, the modes in the two cases would coincide.

That the curves we are about to consider are not merely distribution curves of random sampling in relation to reaction is shown by two facts. Firstly and most important is that the curves for the different species do not exhibit modes corresponding to the same  $pH$  value as would be the case if they were determined by the frequency of soils of a particular reaction. On the contrary, the modes are widely separated over the scale of reaction, the mode for *Psamma arenaria* being in the neighbourhood of  $pH$  7.1 and that of *Pteridium aquilinum* corresponding to  $pH$  5.5. Secondly, some of the species exhibit a curve of bimodal form, whereas the soil curve is monomodal.

The curves for the different species fall into two categories. One type, illustrated by *Pteridium aquilinum* (Fig. 1), *Vaccinium myrtillus* (Fig. 2), *Scilla nutans* (Fig. 3), approximate closely to the normal variation curve with a single mode, and it is noteworthy that in these species the soils examined were almost all on the acid side of the neutral point. In the case of both *Scilla* (Fig. 3) and *Vaccinium* (Fig. 2) we note the suggestion of a bimodal form which may, however, be due to the small number of localities examined, only 62 in the case of *Scilla nutans*. It should, however, be noted that this latter represents about 200 samples. The curve for *Psamma arenaria* (Fig. 4), based in this case on a large number of samples from a single area, shows a similar type of curve with the mode on the alkaline side of the neutral point. Here too we note the suggestion of a second mode between  $pH$  6 and  $pH$  6.1. Broadly speaking, these curves represent not only the incidence frequency but also the frequency of the species in relation to reaction, as in nearly all cases the number and vigour of the individuals is notably less in the localities corresponding to extreme values.

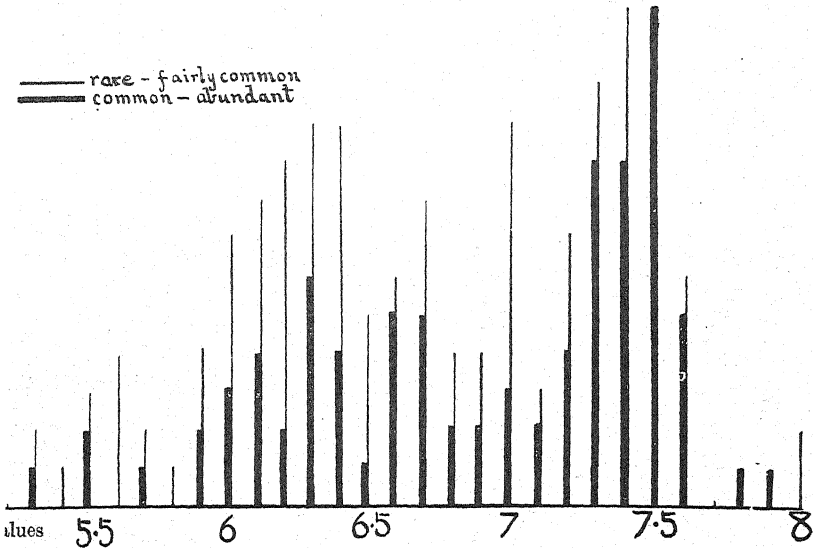
The second type of curve is presented by species such as *Mercurialis perennis* (Fig. 5), and *Ficaria verna* (Fig. 6), where the curve is markedly bimodal in character, the species being most frequent in locations of slight acidity or slight alkalinity.

It is significant that this bimodal curve has also been noted by Hikson, Arrhenius<sup>1</sup> and others in reference to the vigour of species in relation to varying  $pH$  concentrations.

Arrhenius, for example, working with wheat in water cultures ranging from  $pH$  4 to  $pH$  10, obtained a maximum dry weight of the entire plants at

<sup>1</sup> *Journ. Gen. Phys.* 5, 81-88, 1922.

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5. *Mercurialis perennis*. Variation in Hydrogen-ion concentration for 150 Localities.

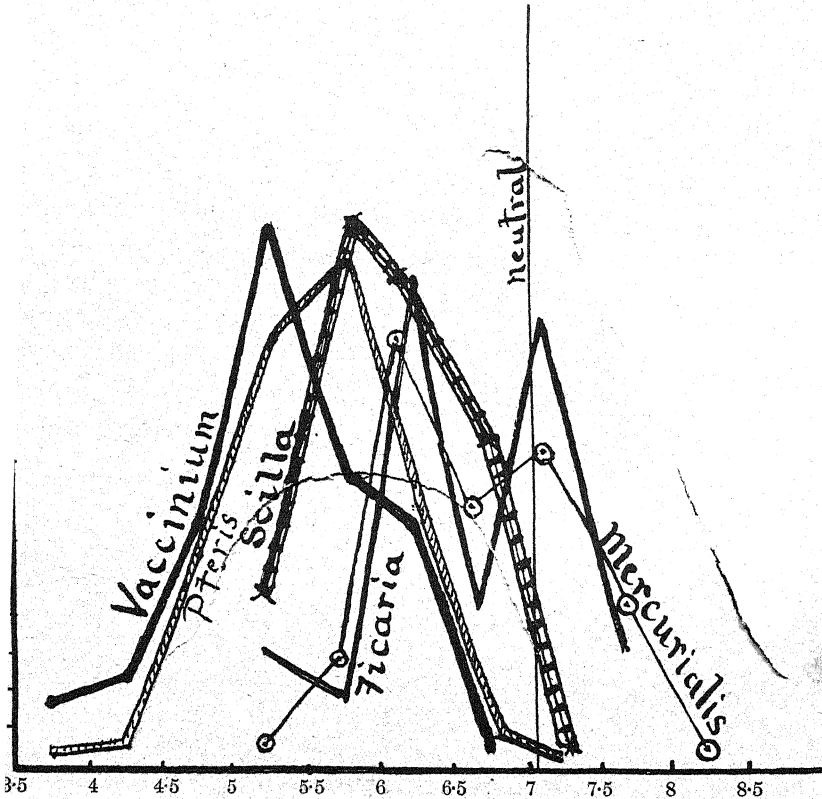


FIG. 6. Percentage frequencies of five species according to grouped pH values.

pH 5 and pH 9. These are also approximately the reaction values for maximum water absorption and almost minimal salt absorption. Similar results were obtained with *Raphanus*, where the dry weights likewise yielded a bimodal curve (cf. Fig. 7).

That competition in nature is largely a function of the rate and vigour of growth is a necessary corollary of the fact that success in the struggle for existence is so often a matter of suppression of one species by another. If, then, there are two regions on the scale of reaction where maximum growth occurs it is reasonable to suppose that these reactions would also correspond to the most successful struggle with competitors in nature and hence a bimodal form in the curve of incidence. Robbins<sup>1</sup> has recently suggested that this bimodal form may be correlated with the isoelectric resultant of the complex of ampholytes represented by the protoplasm. The curves for arboreal species show a similar form. As in the other species, the curves are based on samples 0-6 ins. in depth. The assumption being as appears justified by forestry experience that it is the character of the surface soil which mainly determines success or failure in the early stages of development. It is fully recognised that the incidence curves represent the summation of the effects of both acidity direct, and its indirect effect on other factors. Amongst the indirect effects of acidity may be cited the bringing into solution of acid soluble toxic salts. Such are the salts of aluminium hydroxide and the ferric and ferrous compounds. Aluminium hydroxide is, however, precipitated between pH 3.9 and pH 6.4. In minute quantities aluminium salts are definitely beneficial, hence if aluminium salts were alone concerned in the effects produced by soil reaction we should expect to find species attaining their maximum somewhere about pH 6. Similarly, ferric salts are precipitated between pH 3.5 and pH 6<sup>2</sup> and ferrous salts between pH 5.1 and pH 8. The small amounts of ferrous salts present above pH 6 is probably barely sufficient at the higher values to maintain the requisite supply of iron, hence the tendency towards chlorosis in alkaline soils. Alike, however, for aluminium salts, ferric and ferrous salts, the major part is precipitated between pH 6 and pH 7, so that the bimodal curve cannot possibly be explained as due to the indirect effect of reaction on their solubilities.

It is probable that the effect of acidity is largely an indirect one as it affects the availability of nutrient ions but, as the investigations of Waynick have shown, it is by no means necessarily the conditions which are most favourable for absorption of salts which are most favourable for the growth of the plant<sup>3</sup>. Miss Irwin<sup>4</sup> has shown that the permeability of living cells of *Nitella* to dyes increases with the increasing alkalinity of the medium and it would appear from her work that a considerably higher reaction outside the

<sup>1</sup> *Amer. Journ. Bot.* **10**, 412-439, Oct. 23.

<sup>2</sup> Cf. Patten, H. E. and Mains, G. H. *Journ. Ass. of Agric. Chem.* 1920.

<sup>3</sup> Cf. *Univ. Calif. Pub. Agric. Sci.* **3**, 1918.

<sup>4</sup> *Journ. Gen. Phys.* **5**, 223-4, 1922.



all than inside may be necessary for the optimal absorption of some substances. The results indicate the fallacy of the argument that low pH values cannot be detrimental to the plant because the cell sap has a similarly high acidity.

It has long been recognised that the relative rates of leaching of the nutritive salts in the soil varies greatly. That for instance calcium bicarbonate leaches most rapidly under the influence of carbonated rain water, that potassium and magnesium salts leach out much more slowly.

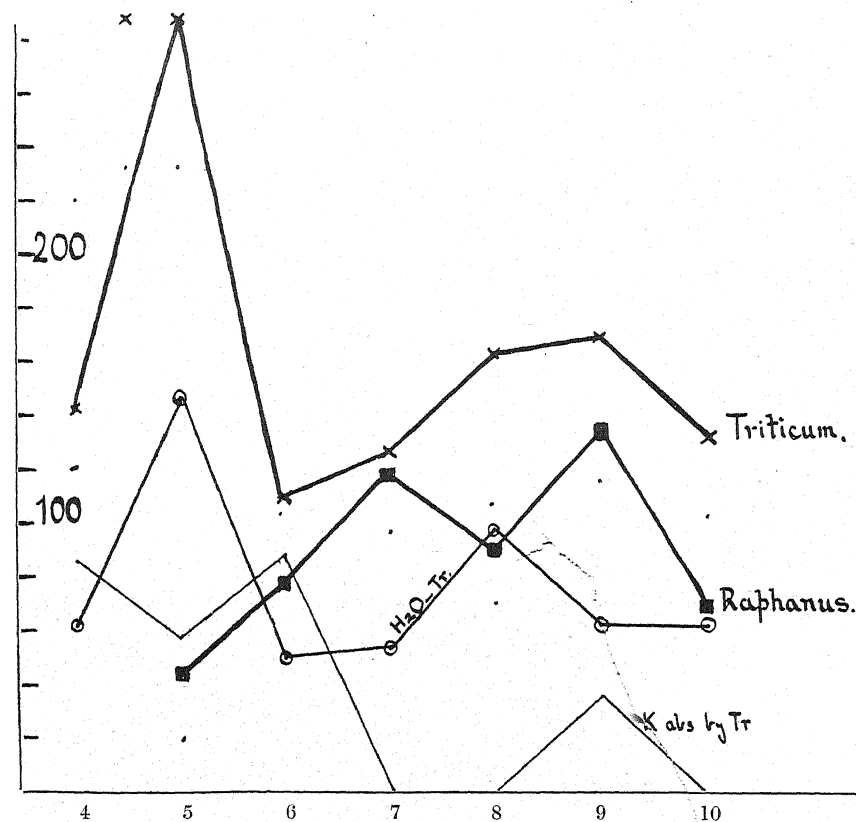


FIG. 7. Dry weights of wheat and radish and absorption of  $H_2O + K$  by wheat at different Hydrogen-ion concentrations (after Arrhenius).

Tansley and the writer<sup>1</sup> found that in some of the Malvern woods on lime-subsoil this differential leaching had led to an actual concentration of potassium and magnesium in the surface layer, and even over subsoils not retaining a high proportion of calcium the most completely leached soils, which are also usually the most acid, tend to be those relatively richest in potassium. Thus there is a tendency for relative increase in potassium to go hand in hand with acidity and the question arises as to whether the effects

<sup>1</sup> This JOURNAL, 9, pp. 23 and 24.

we have attributed to acidity may not really be due to the parallel increase of potassium.

In dealing with the calcicole habit<sup>1</sup> the writer emphasised the importance of Fernald's observations made some 17 years ago, which in conjunction with more recent work indicates that the calcifuge species are in part at least plants demanding a considerable supply of potassium.

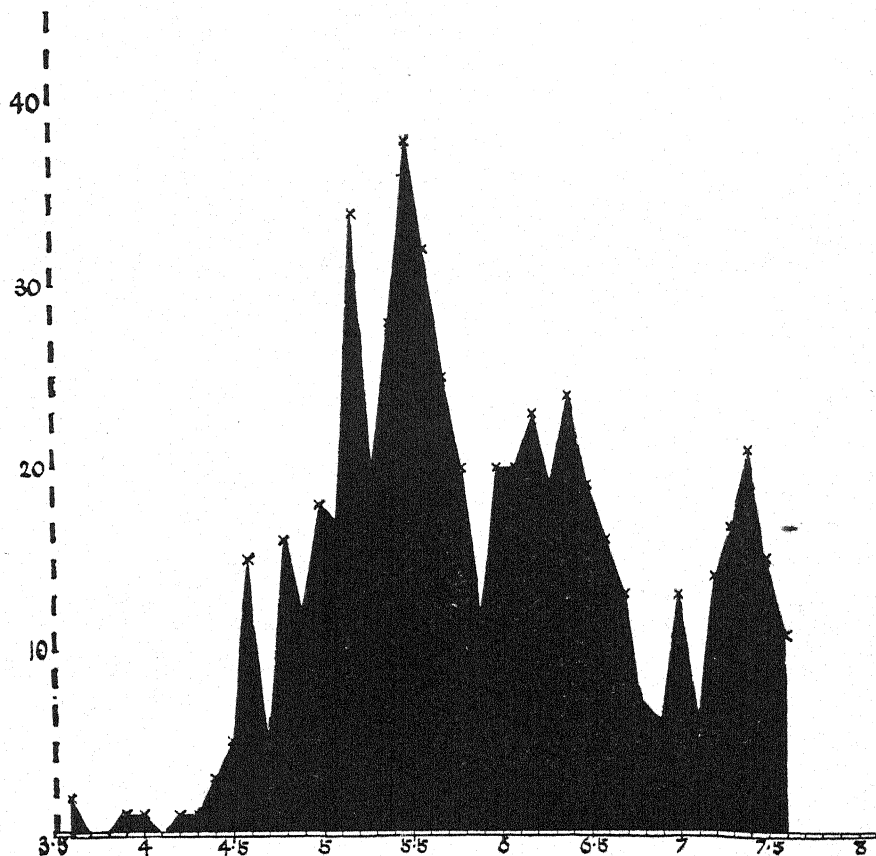


FIG. 8 Variation of Hydrogen-ion concentration in 570 localities of *Quercetum sessiliflora*.

Recently this idea has been developed by Pearsall in a special form, attaching paramount importance to the ratio between *calcium and sodium* and *potassium and magnesium*.

It is obvious that the ordinary chemical analysis is valueless in this connection. Just as the *potential* acidity of some weakly ionised soil acid has little bearing, if any, on the distribution of vegetation, so too it is patent that the proportion of potassium and other salts *actually present in the soil solution* is the essential factor, and this, as is well known, cannot be inferred from chemical analyses. Ratios based on such data moreover yield values that

<sup>1</sup> This JOURNAL, 8, p. 206.

## The Incidence of Species in Relation to Soil Reaction

ously have no relation to the plant covering (the ratio for potassium to sodium, for example in Pteridum, may range from 0.8 to as much as 14.9). Determinations based on the actual soil solution, however, yield the surprising and interesting result that the absolute and relative proportion of mineral salts appears to be subject to surprising fluctuations of considerable

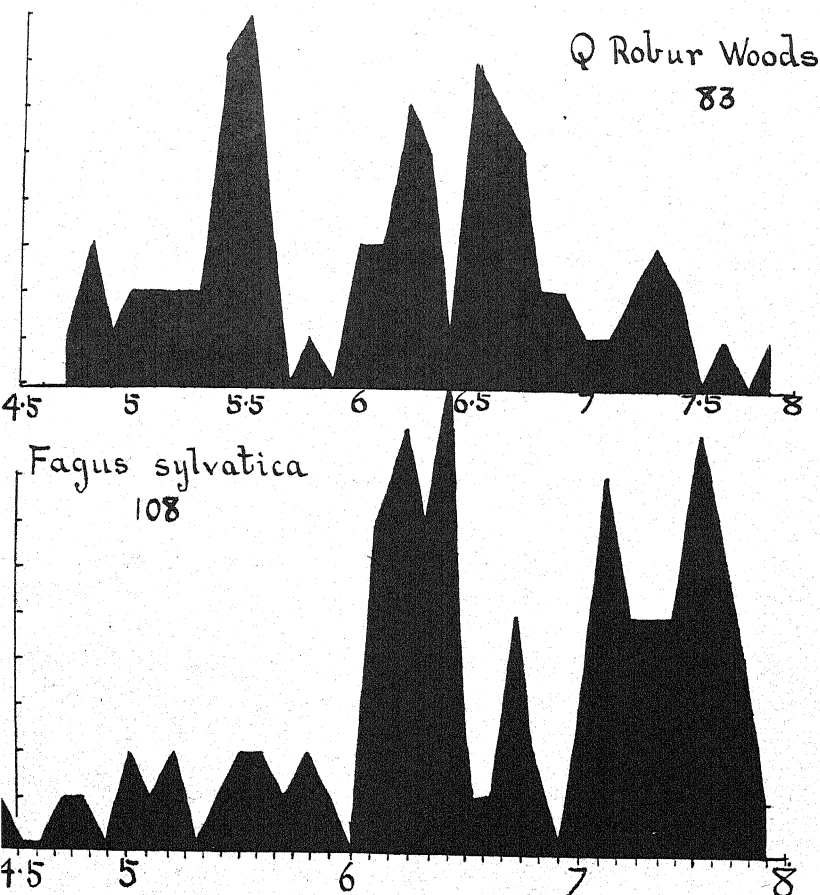


FIG. 9. Variation in Hydrogen-ion concentration in 83 different *Quercus robur* woods and in 108 Beechwoods.

itude in relation to the water content. In 1:5 water extracts Burgess<sup>1</sup> that the ratio of Ca to K may be only 1.6, whereas in the soil solution the ratio was more than three times that value, viz. 6.2. In the seven types studied by him the average ratio was nearly three times as great as the soil solution as obtained by pressure and one must therefore conclude that the relative proportions of the mineral salts are liable to considerable variations with the changing water content. On *a priori* grounds then it would seem more likely that the vegetation should be correlated with the

<sup>1</sup> *Soil Science*, 14, 3.

relatively constant reaction than with a ratio which exhibits marked fluctuations. We could at all events only judge, as in the case of water content, from an extended series of determinations over a considerable period. But even if we knew the ratios in the soil solution it appears that the proportion

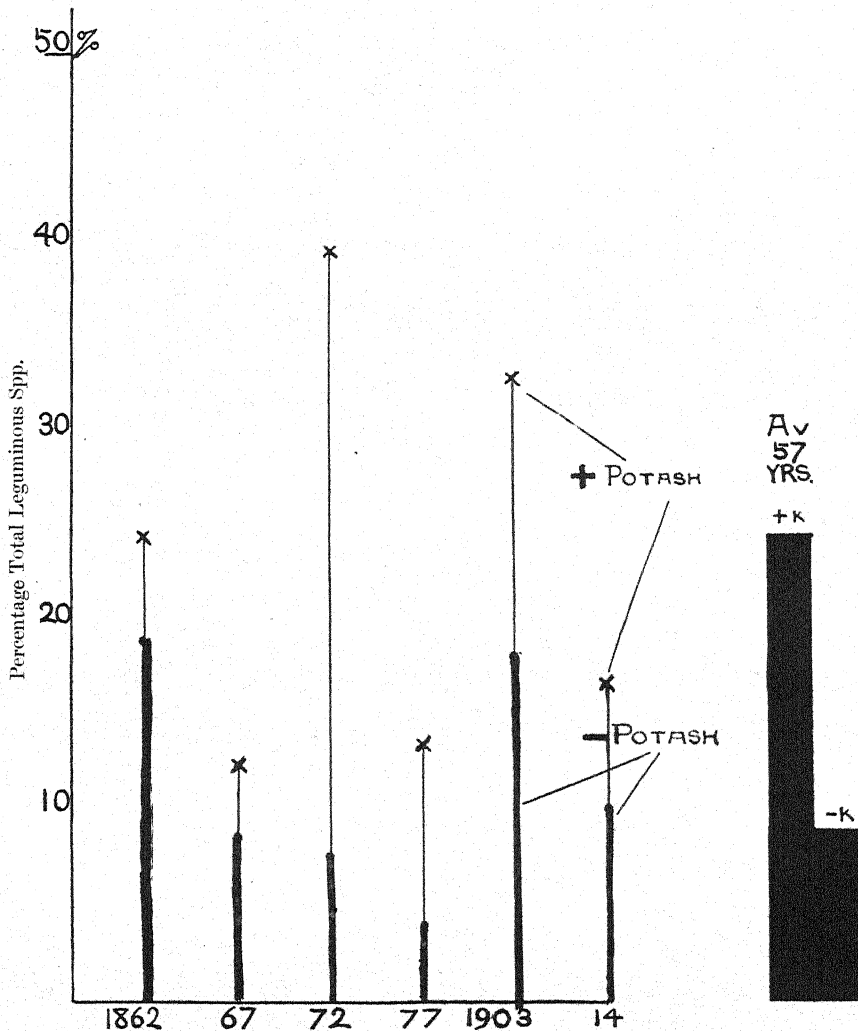


FIG. 10. Mineral Manure with and without Potash. Composition of herbage.

in which the ions are absorbed is not determined by the proportions in which they occur so much as by the reaction of the medium, hence we are again forced back on the pH value of the soil. In the absence of any extensive data on soil solutions we may note that in water cultures of wheat exhibiting a wide range of basic ratios (0.1-3.9) Masall obtained dry weights which when

otted fluctuate quite irregularly about a mean, whereas when grown in cultures of varying pH values a definite optimum is evident.

The hypothesis further involves the assumption that plants of calcareous soils are intolerant of a high proportion of potassium. When, however, the basic ratio is experimentally changed vegetation changes occur which are the reverse of those which should result if the ratio of potassium to the other elements, and not the reaction, is the important factor in determining the character of the vegetation.

The experiments at Rothamsted, which are the longest continued ecological experiments we can quote, include two plots similarly manured, except that one receives potash and the other does not (Fig. 10). After 57 years this has brought about changes of which the most marked is an increase of leguminous plants, characteristic of less acid soils, on the plot receiving potash. Experiments in the United States carried out by Skinner and Noll on 66 plots showed an increase of clovers *on less acid plots* receiving chiefly potassic fertilisation, whilst *on the more acid plots* receiving mainly phosphatic fertilisers the yield of clovers was much lower. Finally, it may be recalled that though chalky soils respond well to potassic manures, many sandy and highly siliceous soils respond equally to this treatment.

One can therefore only conclude that for land plants the basic ratio has little if any significance, and that the main factor which is responsible for the incidence of species is the reaction of the soil, which is one of the several important factors that govern the distribution of plants in the wild state.

## SOME IMPRESSIONS OF THE INTERNATIONAL PHYTOGEOGRAPHICAL EXCURSION IN SWITZERLAND, 1923

By E. J. SALISBURY.

The International Phytogeographical Excursion to Switzerland in July and August 1923 was attended by twenty-eight ecologists (or, as the Swiss and others prefer to call them, Geobotanists) in addition to the Swiss leaders and those with special local knowledge who joined the party temporarily. In all some fifty were for a time at least members of the party, which was remarkable for the number of active workers of which it was composed not less than for the number of nationalities represented, of which there were no less than seventeen.

Despite so many nationalities and the diversity of temperaments the extremely harmonious relations of the entire party made one of its most striking and pleasant features, due in no small measure to the personality of Professor Schröter. In this connection one is glad to have the opportunity to record the debt of gratitude that all those who took part owed to the organising ability of Professors Schröter, Rübel, and Brockmann, and to their unflinching kindness.

One great value of so cosmopolitan a gathering of active ecologists was the occasion it afforded for the discussion of points of view and methods of investigation. It is natural and indeed even desirable that the mode of approach to ecological problems should be different in different countries, but it is a concomitant of the youth of the subject that the various avenues of approach have as yet been followed by the respective schools of ecological thought to such varying degrees that discussions on the classification of plant communities are apt to be more polemical than practical. This impression, which is obtained from a perusal of the literature of the subject, received full confirmation from the numerous discussions that took place, and it became apparent that one cannot at present expect any marked uniformity in regard to synecological treatment. The analogy with the history of the development of a natural classification of plants is calculated to curb any impatience one may feel, since after a much longer period of time we still find that the term species connotes aggregates of very varied taxonomic significance.

In view of the excellent monographs that are now available dealing with most of the areas visited no useful purpose would be served by giving any general description of the vegetation types examined, but it may be useful to draw attention to several special points noted during the excursion.

One of the earliest visits was to the mixed woods near Zurich. These

consist chiefly of Spruce and Beech, but as a consequence of felling and the differential sprouting of the constituent species the mixed wood becomes locally replaced by almost pure stands of *Fagus sylvatica*. Where the Spruce is the dominant tree a sparse ground-flora obtains, but on the light patches, where trees have died through the attack of *Trametes radiciperda*, colonisation takes place by *Carpinus betulus*.

A number of extremely interesting experiments were seen at the Experimental Forestry Station. Amongst these some of the most striking were the experimental plots of *Quercus robur* and *Quercus sessiliflora* grown on various types of soil and affording confirmation of the presumed soil preferences of these two species as deduced from their natural occurrence. On soil rich in calcium, for instance, the vigorous growth of *Q. robur* was in marked contrast to the stunted appearance of its congener on the same type of soil despite the fact that the number of *Quercus sessiliflora* seedlings were fewer and competition consequently less keen. On soil rich in humus *Quercus sessiliflora* had the decided advantage, whilst on gneiss there was no difference sufficiently great to be recognised visually.

Other plots had been sown with Spruce seed collected from different altitudes. The resultant trees were very different in height and in general their stature showed a decrease with the increasing altitude of the source of the seed.

In the Laboratory were exhibited a number of diagrams showing heliotropism in tree trunks, the movement amounting in some cases to 26° in four years.

During the stay on Mt. Pilatus, where the slope was gentle and on isolated grassy hummocks, interesting examples of leaching were seen. In such spots the characteristic calcicole vegetation of the steeper slopes gave place to calcifuge elements in which *Nardus stricta* and *Astrantia minor* were conspicuous features. A similar but even more striking instance was encountered near Lugano where on Monte Salvatore a comparatively level stretch of leached surface soil bore *Pteridium aquilinum* and *Calluna vulgaris*. On digging up specimens of the latter it was found, as in similar cases examined in this country, that the roots penetrated into the highly calcareous sub-soil.

On the way from Zurich to Thusis a halt was made to examine a Fen community very similar to an English "Low Moor" with *Parnassia palustris*, *Molinia coerulea*, *Poterium officinale*, *Epipactis palustris*, *Orchis incarnata*, *Peucedanum palustre*, and many other British Fen plants including, the now extinct, *Senecio palustris*. In these familiar surroundings it was therefore the more surprising to see *Herminium monorchis*, a species we associate with dry chalk pastures, in waterlogged soil side by side with *Rhynchospora alba* and *Spiranthes aestivalis*. Similar instances are known in our own vegetation and probably the same explanation holds (cf. this JOURNAL, 4, p. 99 and 8, p. 210). Our sand-dune shrub *Hippophaë rhamnoides* was seen in

this same area growing as a fen species, which recalls the observation of Kingdom Ward (*Land of the Blue Poppy*) that this shrub forms dense thickets on an alluvial fan at Tsa-lei at 13,000 ft. and grows by the side of all the more sluggish streams of south-eastern Tibet. On Mt. Pilatus *Hippophaë* is likewise met with quite near the tree limit.

On the way to visit the beautiful National Park in the Lower Engadine the party stayed at Zernez, which has a decidedly continental climate with a mean temperature of about 21° C. and a rainfall of about 28.7 ins. The steep slopes behind Zernez have a southerly aspect and bear a very xerothermic flora that contains many elements in common with the sandy heaths of Suffolk, where also there is a low rainfall in relation to the mean annual temperature. Amongst the species characteristic of both areas may be mentioned *Artemisia campestris*, *Koeleria gracilis*, *Medicago falcata*, *Onopordon acanthium*, *Phleum Boehmeri*, *Scleranthus perennis* and *Veronica spicata*. These species mostly belong to the Pontico-sarmatian group of Sterner (*Geografiska Annaler*, 1922) with a distribution mainly centered in southern and central Europe.

In the National Park itself an interesting intermingling of calcicole and calcifuge species appeared to be correlated with topographical changes that suggested differential leaching of the surface. Further on, the slopes of Buffalora exhibited an exceptionally high tree-limit at an altitude of 2300 m. and beautiful examples of the prostrate form of *Pinus montana* up to 2350 m. Here too was seen a good instance of the recession zone of the tree limit, occupied by *Rhododendron*, etc.

A week's sojourn in the Bernina Hospice admitted of a close study of some of the high alpine vegetation, and particularly of the peculiar vegetation of the "Schneetälchen" in which *Anthelia julacea* was a constant and characteristic feature. It was interesting to note the regular presence of *Salix herbacea* and *Gnaphalium alpinum* as in the snow-flushes of Scotland (cf. W. G. Smith, *Scot. Bot. Rev.* 1912).

In the Heutal, famous for its alpine pasture, the underlying rock is mainly non-calcareous but on one side of the valley calcareous strata are exposed and produce "flush" effects in the pasture below, with a corresponding admixture of calcicole species, which diminishes as the distance from the calcareous rocks increases.

The flat roof of the Bernina Hospice offered an interesting example of colonisation by wind borne seeds. Here were present a number of plants of *Poa alpina*, *Cardamine resedifolia*, and two of *Festuca rubra*, but the number of dead individuals bore witness to the rigour of the habitat. Behind the Hospice Prof. Brockmann demonstrated the erosion of soil and vegetation on slopes which had remained unprotected by the snow during the winter storms.

On leaving the Bernina Hospice en route for Italy the foot of the Palu glacier was passed. This presents a wonderful succession of terminal moraines,



corresponding to the gradual recession of the glacier. These moraines have each been colonised in turn by *Larix europea* from the neighbouring forest, the outermost moraine bearing large trees whilst those on the youngest moraine are still comparatively small. Here too are to be seen beautiful examples of the avalanche gullies colonised by *Alnus viridis*, appearing as bright green vertical streaks interrupting the forest of Larch.

On crossing the frontier into Italy the prevalence of the Peruvian alien *Galinsoga parviflora* by the wayside was noteworthy, whilst *Setaria viridis* and *Setaria verticillata* were the conspicuous weeds of the cultivated fields of *Sorghum*, Buckwheat and Tobacco. The dry slopes of siliceous soil exhibited a large proportion of continental types and in addition to calcifuge species such as *Pteridium aquilinum*, *Calluna vulgaris*, *Jasione montana*, etc., there were present others such as *Silene nutans*, *Carlina vulgaris*, and *Galium cruciatum*, which in more northern climes tend to be restricted to calcareous soils where perhaps the physical rather than the chemical conditions determine their habitat.

Towards the end of the excursion a visit was paid to the Lauterbrunnen valley where, below the talus of calcareous rock covered with *Stipa calamagrostis*, there grew a scrub of *Corylus avellana* in which the ground flora was very similar in composition to that of our own chalk scrub but with the addition of southern types such as *Erica carnea*, *Hepatica vulgaris*, *Vincetoxicum officinale*, etc.

On the Lauberhorn the stone slides recalled our English shingle beaches, the rôle of *Suaeda fruticosa* in holding back the stones being here played by *Vaccinium uliginosum*, which reacts in a similar way to burial by rock fragments.

It need hardly be emphasised that only a very few features that impressed the writer as of particular interest to the student of British ecology have been mentioned and nothing has been said of the many equally striking examples of syn-ecological and aut-ecological phenomena of wider appeal, since most of the latter are dealt with in Prof. Schröter's *Pflanzenleben der Alpen* (of which a new edition is now available) and the admirable monographs published under the auspices of the Pflanzengeographische Kommission der Schweiz.

Professors Schröter, Rübel and Brockmann were appointed as a permanent committee to serve as a central body for these International Excursions and a majority of those present passed a resolution in favour of biennial excursions. The next of these it is proposed to hold in Norway and Sweden in 1925.

## THE IMPERIAL FORESTRY INSTITUTE, OXFORD

(COMMUNICATED)

Last year saw the beginning of what should prove to be a great development in Forestry training and research, with the establishment at Oxford of an Institute which will be known as the Imperial Forestry Institute, a title adopted at the command of His Majesty the King.

The question of establishing a central training institution was first discussed by the British Empire Forestry Conference in 1920. This Conference felt that, owing to lack of funds and dissipation of effort, training in the higher branches of forestry for the needs of the Empire was nowhere as complete or efficient as was desirable, and therefore recommended the establishment in the United Kingdom of one institution which should undertake the higher training of forest officers and should also be a centre for research into the formation, tending, and protection of forests. An impartial Committee, consisting partly of representatives of Government departments concerned and partly of experts, was thereupon appointed to make recommendations regarding the location and organisation of such an institution, and other matters. After visiting the Universities of Oxford, Cambridge, Bangor, and Edinburgh, and also taking evidence from other Universities, as well as from Institutions and Societies interested in forestry, this Committee issued in 1921 a report which recommended the establishment at Oxford of a central institution for the higher training of forest officers, for training in research, for the provision of special and "refresher" courses for officers already serving, and for the conduct of research into forest production. The report made it clear that there was no intention of interfering with the work done by the various University Schools of Forestry, and provided the training of these was maintained at a required standard, selected students from any such schools would be eligible for admission to the central institution. Full details will be found in the Report of the Interdepartmental Committee on Imperial Forestry Education, 1921 (Command Paper 1166).

Further action was suspended until 1923, when the proposals of the Interdepartmental Committee were considered by the British Empire Forestry Conference in Canada. The Conference supported them in the strongest terms and they were subsequently endorsed by the Imperial Economic Conference held in London the same year. Arrangements were accordingly completed for starting the Institute in October 1924.

The Imperial Forestry Institute will be a University Institution, the Professor of Forestry being its Director. It will be under the control of a Board of Governors representing the University and Government Departments concerned, under the Chairmanship of Lord Clinton, a Forestry Commissioner. The educational work of the Institute will comprise (1) post-graduate training of probationers for the forest services and of other qualified persons, (2) training of research officers in special subjects, and (3) provision of courses for selected officers already serving. It is intended that the Institute should maintain close touch with and be of assistance to the various forestry training centres throughout the Empire. Thus, in the case of overseas training centres which have no direct means of giving practical instruction in the latest systems of management as practised on the continent of Europe, it will be one of the functions of the Institute to arrange for such practical instruction to be given by members of its own staff to students who have already completed their general course of training at their own Universities or Colleges.

If in any particular case it cannot undertake to give direct instruction, the Institute may arrange that this should be given at some other place. It is proposed, for instance, that close touch should be maintained with the Royal Botanic Gardens, Kew, whose unrivalled resources should be of great assistance to those students who may wish to study systematic botany and economic products. Again, forest engineering is a subject which cannot be dealt with comprehensively in Great Britain, owing to the absence of logging

operations on a large scale; arrangements will therefore be made as far as possible to study it practically in the forest regions of the Continent, or in certain cases in Canada. Similarly, the study of tropical silviculture from the practical point of view is impossible outside the tropics, and hence the Institute will maintain close touch with other institutions where this subject can be efficiently dealt with, such as the Forest Research Institute and College, Dehra Dun, in order that the best possible arrangements may be made in the interests of students who wish to make a practical study of tropical silviculture.

Although the Institute is intended primarily to serve the needs of Forestry in the British Empire, it will be open to qualified students of any nationality provided that there is sufficient accommodation. Nor is it by any means intended that it should cater only for the requirements of State forest services; now that timber and wood-pulp firms are becoming more and more interested in the management and working of forests on scientific and economic lines, the Institute should be of special value in providing them with fully trained employees. Students admitted to the Institute may, in fact, be included under any of the following categories:

(a) Those possessing a Degree in Forestry, or a Diploma or equivalent certificate of having satisfactorily completed an approved course of training in forestry, who have been selected as probationers for the higher branch of some forest service.

(b) Graduates with honours in Science, who desire to become specialists in some branch of work connected with forestry.

(c) Forest officers deputed to attend courses with the view of bringing their professional knowledge up to date.

(d) Students of approved qualifications not included in the first three categories, who are admitted on the recommendation of overseas governments.

(e) Students with a University training in forestry who may wish to attend the Institute on their own account and at their own expense.

The course of study at the Institute will normally extend over one academic year, beginning October, and will be made sufficiently elastic to serve the needs of individual students. The subjects dealt with will cover the whole range of Forestry, and will include Silviculture (European and Tropical), Forest Management (including Mensuration, Valuation, and working plans), Forest Botany (including physiology and anatomy of trees, mycology and pathology, ecology, and systematic botany), Forest Zoology (including entomology), Forest Utilisation (including the structure, properties, and uses of wood), Soils, Climatology, Forest Economics and Policy, Forest Law, and Forest Engineering, including Surveying.

Temporary accommodation for the Institute has been arranged in the University School of Forestry building, but a more suitable site and larger buildings will be necessary, and the formidable task of obtaining funds for the acquisition of a site and the erection of buildings remains. A building fund is being started, and it is hoped that this great undertaking will not suffer from lack of support on the part of benefactors who have at heart the welfare of the Empire in general and the cause of Forestry in particular.

The Institute started work on October 13, in the School of Forestry building until arrangements can be completed for the erection of new buildings on another site.

The following Staff has already been appointed: Director, Professor R. S. TROUP, C.I.E., M.A., D.Sc.; Secretary, Mr P. S. SPOKES, B.Sc., M.A.; Lecturers—Economics of Forestry, Mr W. E. HILEY, M.A.; Silviculture, Mr H. G. CHAMPION, M.A.; Mycology, Mr W. R. DAY, B.A., B.Sc.; Structure and Properties of Wood, Mr L. CHALK, B.A. Other posts have yet to be filled. The Institute will, in addition, have the assistance of the following members of the Staff of the School of Forestry: Forest Management, Mr R. BOURNE, M.A.; Surveying and Engineering, Mr N. F. MACKENZIE, Hon.M.A. The Forestry Commissioners have agreed to station at the Institute certain of their research officers. In spite of the fact that the Institute is not yet fully organised and that sufficient time has not yet elapsed for the attendance of students from all parts of the Empire, nine students, deputed by the Colonial Office and the Forestry Commissioners, have begun special courses, and further students are expected to join during the next few months.

# BRITISH ECOLOGICAL SOCIETY

## SUMMER EXCURSION 1924

A party of ten visited the Gower Peninsula, in Glamorganshire, South Wales, from September 1st to 6th. The weather was very favourable and an interesting week resulted. The extreme length of the peninsula from Swansea to Rhossili is about 17 miles and its average width 6 miles; yet, in spite of its proximity to the Welsh coalfield, it is visited much less than its natural beauty deserves; possibly owing to the absence of any railway communications within the peninsula itself.

The party made their centre at Reynoldston, from which each quarter of the area was explored in turn. The ecological interest derives in part from the varied habitat conditions which exist. Geologically there is a sharp division between the acidic coal measures sandstones at the east end, with *Q. sessiliflora* woods and dry grass heaths; and the limestone which composes the west, with ash and oak-ash woods and extensive arable. Westwards also, post-carboniferous folding has thrown up several ridges of Devonian conglomerate of a highly quartzose character, which also shows, in its peaty heaths, a marked contrast with the surrounding limestone.

The coast is of very various nature, principally limestone cliff, partly overlaid with a shallow heath-bearing soil but carrying also ashwoods, dense scrub and a rich ledge-flora, including *Helianthemum canum*, *Asparagus maritimus*, *Draba aizoides* (the only British habitat) and several woodland plants, e.g. *Ruscus aculeatus*. There are extensive fresh and salt marshes, where *Althaea officinalis* provides a fine spectacle, and areas of high, blown sand, overlying limestone, as well as more normal dune systems, which Dr Salisbury considered to show a very close resemblance to those of the Lancashire coast.

At Llanmadoc *Aconitum napellus* was seen abundantly in the corner of a field, some 40 miles away from its main locality on the Ely River, near Cardiff. On Worm's Head it was surprising to see beds of luxuriant grasses on a peaty basis into which a stick could be thrust for nearly 18 ins., developed at an altitude of only 50 ft. above sea level and on a fully exposed S.W. slope. There appear however to be neither sheep nor rabbits on this part of the Headland, which is practically an island. On the cliffs opposite, which are exposed to grazing and nibbling, the turf is very short.

The area was for the most part, of necessity, only examined cursorily. Several special features were however studied in greater detail and a few notes on these may be placed on record.

The interesting dune system known as Whitford Burrows was noteworthy for the high proportion of calcicole species, particularly on the more stable yellow-dune phase. The early phases exhibited a very high calcium content and samples taken showed a range of from 11.8 to 13.5 per cent.  $\text{CaCO}_3$ . The source of the comminuted shell fragments was not far to seek, as considerable deposits of shells were exposed in some of the dune hollows consisting chiefly of *Cardium edule* and *Helix nemoralis*. The older phases bearing the high proportion of calcicole species were also sampled and showed a calcium content of over 3 per cent.

In the dune slacks the following species were listed by Mr Hyde and one of the writers:

- Agrostis maritima l.ab.
- × Anagallis tenella c.
- × Chlora perfoliata o.
- Epipactis palustris l.c.
- × Erythraea pulchella f.
- × " umbellata l.
- × Euphrasia ? nemorosa o.
- × Gentiana amarella r.r.
- × Glaux maritima f.

- × Hydrocotyle vulgaris f.
- Hypericum tetrapterum r.
- × Juncus acutus l.f.
- " lampocarpus.
- Leontodon autumnale.
- Linum catharticum.
- × Mentha aquatica.
- " arvensis.
- Plantago major r.

- |  |  |
|--|--|
| × <i>Plantago coronopus</i> f. <i>pygmaea</i> .  | <i>Senecio jacobaea</i> f.                         |
| " <i>maritima</i> .                              | <i>Trifolium dubium</i> r.r.                       |
| × <i>Potentilla anserina</i> .                   |  |
| × <i>Sagina nodosa</i> c.                        | <i>Equisetum variegatum</i> v. <i>arenarium</i> r. |
| <i>Salix repens</i> c.-ab.                       | <i>Aneura pinguis</i> .                            |
| × <i>Samolus valerandi</i> l.c. (wettest parts). | × <i>Petalophyllum ralfsii</i> l.c.                |
| <i>Scutellaria galericulata</i> r.r.             | × <i>Nostoc</i> sp. (? <i>vulgare</i> ) ab.        |

The species marked with a cross are recorded by Watson (this JOURNAL, 6, 126-143) as present in the slacks of Braunton Burrows.

Whilst the above list is probably incomplete it has been given in full to emphasise the resemblance of these slacks to those of the Lancashire dunes. This is perhaps best realised from the fact that all the above species have been found by the writer in the dune slacks near Freshfield.

This correspondence is the more significant in that several of the plants named are local or rare. *Juncus acutus*, which is here frequent (the writer also noted it in some abundance in dune slacks at Borth-y-Gest, N. Wales), is very rare on the Southport system and on the other hand *Parnassia palustris* and *Pyrola rotundifolia* v. *maritima*, which are both so marked a feature of the Lancashire dunes, are here absent.

Striking features of the slacks at Whitford were the depauperate ecads of several species of *Plantago*, notably *P. major*, which occurred less than an inch in height and with an inflorescence reduced in some examples to only two flowers.

On the occasion of the visit to Worm's Head the calcareous pasture on the adjoining coast was examined in detail over a small area. In one part, where the slope changed from a steep angle to a gentle one, several patches of very dwarf *Calluna*, accompanied by *Scabiosa succisa*, were noted. Soil samples taken in these patches showed that the soil here had been very much leached, but that the downwash of soil particles from above had caused a reversal of the normal carbonate gradient in the surface layers comparable to that recorded by the writer for the foot of a slope at Hudnall Common in Hertfordshire (cf. this JOURNAL, 9, p. 231).

Carbonate content of successive samples from *Calluna* patch:

Depth	0-2 ins.	0.15 per cent. CaCO <sub>3</sub>
	2-4 "	0.15 "
	5-8 "	0.05 "
	8-10 "	0.02 "

Another interesting feature observed was the presence of *Quercus sessiliflora* on soil derived from Mountain Limestone and presenting well-grown trees and not dwarf specimens such as occur on the Mountain Limestone near Llandudno. On examination of a sample taken at the foot of a *Q. sessiliflora* tree to a depth of about eight inches it was found to contain from 0.09 per cent. to 0.10 per cent. of calcium carbonate, which would seem to indicate that the seedlings at all events are rooted in comparatively leached soil.

R. C. McLEAN.  
E. J. SALISBURY.

## SOIRÉE AT UNIVERSITY COLLEGE, LONDON

On the invitation of the President and Council the members and guests were entertained at a Soirée in the Botanical Department at University College, London, on the evening of Jan. 9th, 1925, the night before the Annual Meeting. About a hundred members and visitors were present and were received by the President, Prof. F. E. Weiss, at the entrance to the Department, whence they passed into the various Laboratories where exhibits were on view.

In the Elementary Laboratory the Director of Kew exhibited a series of rare plants of widely different families showing similarity of xerophytic habit. The Botanical Department of University College, Aberystwyth, exhibited a relief map showing the distribution of woodland types in North Wales and Mr D. A. Jones a series of ecological photographs of the same region.

Prof. Stojanoff of the University of Sofia and Mr W. B. Turrill exhibited a series of plants from the Balkans including many British species amongst which was *Buxus sempervirens* from an altitude of 2000 metres.

Major K. W. Braid showed an interesting series of specimens illustrating the Mycorrhiza of the Oak.

Air photographs of Canadian forests were shown by Mr Hamshaw Thomas and a beautiful series illustrating the vegetation of the Oxford district by Dr A. H. Church.

A series of life-size drawings of the root systems of woodland plants showing their distribution in relation to various soil conditions was exhibited by Dr E. J. Salisbury. Dr Lilian Clarke showed photographs illustrating the colonisation of sand by *Carex arenaria*. Mr Michael Perkins exhibited a series of specimens and maps showing the distribution of the Crab parasite *Sacculina* in the English Channel.

Dr Brenchley and Miss K. Warington showed specimens of Clover illustrating the stimulating effect of boron and Dr Pearsall specimens of *Potamogeton* illustrating that of calcium.

An exhibit of Mangroves, Algae and Karroo plants was shown by Dr Delf.

In the Advanced Laboratory Dr E. J. Collins exhibited forms of *Silene acaulis* and Mr Burt Davy examples of epharmonic convergence in the development of the suffrutescent habit. Prof. Boycott and Mr Diver showed culture forms of *Elodea canadensis* and Mr R. W. Butcher slides illustrative of periodicity in Plankton.

A number of fresh specimens of chalk plants showing the character of the root systems was shown by Miss V. E. L. Anderson, who also exhibited charts of the water content of chalk-down soils over an extended period. Specimens of various soils, their vegetation and reaction, were shown by Mr Chapman.

An extensive exhibit by the Botanical Department of University College showed the development and establishment of vegetation on the Blakeney Far Point, the winter phases of Salt Marsh development from *Microcoleus ethonoplastes* to *Glyceria* sward and *Obione*, and the growth habits of various halophytes. Various states of *Plantago coronopus* were shown including the forma *pygmaea*.

The conditions of preservation of halophytes in salt marsh soils were illustrated by a model and by specimens exhibited by Miss Mottram and Mr Hunter.

In the Library Mr W. Hales showed a series of xerophilous plants and liverworts from the Chelsea Physic Garden.

Dr Woodhead by means of maps and specimens showed the relation of Man to Vegetation in the Huddersfield area and the period of peat formation in relation to Roman and prehistoric remains.

The spread of *Spartina Townsendii*, its habit and related species, were well portrayed by Prof. Oliver and Prof. Mangham.

During the evening Prof. Oliver gave a short lantern lecture on the birds of Blakeney Point, and Mr Hill and Dr Haas gave a demonstration of the colour changes in *Mercurialis perennis*.

Light refreshments were served during the evening by students of the Department; to these and to Miss Anderson the brilliant success of the evening was due in no small measure.

This soirée was the first given by the Society. The members and their friends enjoyed themselves very much, and the hope that other similar entertainments might be given in the future was widely expressed.

## ANNUAL MEETING

The 11th Annual Meeting was held at 10 a.m. on Saturday, January 10th, in the Botanical Lecture Theatre at University College, London. The President, Prof. F. E. Weiss, occupied the Chair.

The minutes of the previous Annual Meeting were taken as read. The Hon. Treasurer then presented the accounts for the years 1923 and 1924 (see pp. 170, 171). He pointed out

# REVENUE ACCOUNT FOR YEAR 1923

<i>Income</i>		<i>Expenditure</i>	
	£ s. d.		£ s. d.
Subscriptions received including Arrears ...	156 15 4	<i>Journal of Ecology</i> (two issues for year)—	
Do. prepaid ...	8 0 0	Paper, Printing and Illustrations ...	353 5 5
Interest on Bank Deposit ...	...	Publishers' Charges and Commission ...	63 4 7
Sale of Reprints—British Vegetation Committee and others ...	...	Insurance of Stock ...	1 19 0
<i>Journal of Ecology</i> —Sales ...	273 11 1	<i>Working Expenses</i> —	
		Postages and Stationery ...	2 17 4
		Printing ...	3 8 6
		Travelling Expenses ...	1 16 6
		Bank Charges ...	1 6 8
			9 9 0
		<i>Balance—Surplus on year—</i>	427 18 0
		Carried to Balance Sheet ...	...
			12 10 3
			440 8 3

## BALANCE SHEET AT 31st DECEMBER, 1923

<i>Liabilities</i>		<i>Assets</i>	
	£ s. d.		£ s. d.
Subscriptions prepaid for 1924 ...	8 0 0	Subscriptions outstanding at 31st December 1923 and since paid ...	...
<i>Journal of Ecology</i> —Cambridge University Press—Balance due to Publishers ...	188 6 5	Westminster Bank—Chancery Lane and Holborn Branch—Credit Balances—	...
<i>General Revenue Account—Balance of Funds:</i>		Current Account... ..	20 12 9
Surplus at 31st December, 1922 ...	50 18 5	Deposit Account... ..	210 0 0
Surplus from Revenue Account for 1923 ...	12 10 3		230 12 9
			259 15 1

NOTE. A further asset is the stock of the *Journal of Ecology* unsold and held for the Society by the Publishers, the Cambridge University Press

HUGH BOYD WATT,  
Hon. Treasurer.

BRITISH ECOLOGICAL SOCIETY

## REVENUE ACCOUNT FOR YEAR 1924

[illegible]BALANCE SHEET AT 31<sup>ST</sup> DECEMBER, 1924

<i>Liabilities</i>		<i>Assets</i>	
£	s. d.	£	s. d.
Subscriptions prepaid for 1925 and 1926 ...	...	Westminster Bank—Credit Balances—	
<i>General Revenue Account—Balance of Funds:</i>		Current Account ...	...
Surplus at 31st December, 1923 ...	63 8 8	Deposit Account ...	...
Surplus from Revenue Account for 1924	29 14 2		...
	93 2 10		...
	106 12 10		106 12 10

I have examined the accounts for the years ending December 31st, 1923, and December 31st, 1924, and certify them to be a correct statement, and that all vouchers are in accordance with receipts and payments shown thereon.

8th January, 1925.

*Hon. Treasurer,*

HUGH BOYD WATT,

**ROBERT PAULSON.**



that he was able to present the audited accounts for the year just closed, a great advantage to the members of the Society, owing to the holding of the Annual Meeting early in the new year, instead of in December as heretofore. The finances of the Society were in a sound state, an especially encouraging feature being the large increase in receipts from the sale of the JOURNAL in 1924. The cost of the JOURNAL however constantly tends to increase, and, especially in view of the desirability of enlarging it, a still larger income is wanted. The Council are therefore recommending that the subscription price to the public be raised, since it is at present unreasonably low. The accounts and report were adopted.

On the proposition of the Chairman a very hearty vote of thanks was accorded to Mr Paulson for auditing the Society's Accounts and on the proposition of Mr Tansley, seconded by Prof. Fritch, Mr Paulson was elected auditor for the year.

The Hon. Secretary then submitted his report for the year 1924, which was adopted.

### THE HON. SECRETARY'S REPORT FOR 1924

Two meetings have been held during the year 1924, the annual meeting, customarily held in December, having been shifted to January.

The chief field meeting was held in the Gower Peninsula with headquarters at Reynoldston from Sept. 1st to Sept. 6th. For the arrangements and leadership of this very successful excursion the Society is indebted to Prof. R. C. McLean (see Report on p. 167).

On October 25th the annual excursion in conjunction with the British Mycological Society was held at Burnham Beeches under the leadership of Mr Ramsbottom.

Two parts of the JOURNAL (constituting vol. 12) have been issued during the past year, the first, consisting of 128, the second of 224, making 352 pages in all. This large second issue was rendered desirable in order to dispose of arrears of papers awaiting publication, and a special donation to the Society's funds was made with that end in view by a donor who desires to remain anonymous. The high standard which our Journal maintains at a subscription price much lower than that of comparable Journals of similar size and character are features which the Society owes in no small measure to the ability and untiring efforts towards economic production of our Hon. Editor. The Council feel that, whilst they do not desire to increase the cost of membership, the price of the Journal to non-members must now be raised.

The number of members remains practically the same. During the past year there have been a rather larger number of resignations than usual, though it is satisfactory to know from the letters received that this is in no way due to any fault of the Society. The membership to January 1st comprises two honorary and 154 ordinary members.

The Council's nominees for office were then elected as follows:

*Vice-President.* Mr T. G. HILL.

*Hon. Treasurer.* Mr H. B. WATT.

*Hon. Editor.* Mr A. G. TANSLEY.

*Hon. Secretary.* Dr E. J. SALISBURY.

*New Council Members.* Professor FRITCH and Dr W. H. PEARSALL.

The following recommendations of the Council respecting alterations to the Rules were adopted:

RULE 3 A. Applicants for Membership of the Society shall be proposed by one member (from personal knowledge) or by an Officer of the Society (without personal knowledge), and seconded by one or more other members. Such applications to be made on a form to be supplied by the Hon. Secretary, and duly filled up and signed by the applicant.

Election shall take place either by ballot at a General Meeting or at other times by resolution of the Council. A majority of votes in favour shall result in the election of the applicant.

That Rule 27 shall read "The subscription price of the *Journal of Ecology* to others than members of the Society is TWENTY-FIVE SHILLINGS per annum, post free."

On the proposition of Prof. Weiss, seconded by Mr Tansley, a unanimous resolution was passed to the effect that a message of greeting from the Society be sent to Prof. Schröter

of Zürich on the occasion of his 70th birthday. The great services of Prof. Schröter to international work and the happy influence of his lovable personality were testified to.

The President then stated that the Council had suggested the election of Prof. Schröter as an Honorary Life Member of the Society. On the proposition of Mr Burt Davy seconded by Dr Woodhead and supported by other members personally acquainted with Prof. Schröter, this was carried unanimously.

The President then proposed from the Chair that the best thanks of the Society be accorded to Prof. Oliver, Dr Salisbury, Miss Anderson and all those who had assisted to make the Soirée of the previous evening so successful.

The President then delivered his Address entitled "Plant Structure and Environment." At its conclusion a hearty vote of thanks to the President was proposed by Prof. Yapp, seconded by Mr Hamshaw Thomas, and carried by acclamation.

The first communication was from Prof. Yapp who described the manner of frost formation on leaves, illustrating his remarks with a series of beautiful photographs. Attention was called to the manner in which hoar-frost begins to be deposited at the edge and on prominences of the leaf and it was suggested that the temperature differentiation indicated might be of considerable significance in the economy of the leaf.

Miss Drew followed with an account of the effect of frost in producing superficial markings on the soil of mountains in the Lake District. Polygons comparable with those well known in Spitzbergen and other Arctic regions were found. Also bands of stones consisting alternately of large and small units were formed parallel to the contours. Of these latter the ridges of large stones become colonised in a remarkably regular manner by *Festuca ovina*.

After lunch in the College Refectory, Dr A. S. Watt dealt with the Yew communities on the Sussex Downs, taking the view that they represent not a climax community but a temporary though long drawn out phase in succession towards woodland. The Yew scrub was regarded as following deciduous scrub and giving place to Ash-Oak and this in turn to Beechwood, though individual yews frequently persist into the climax. Mr Tansley, Mr H. Gilbert Carter (who, on the ground of the well-known passage in Caesar's *De Bello Gallico*, argued that we were not justified in believing that *Fagus* formed woods in southern England in the first century, B.C.) and Dr Salisbury took part in the discussion which followed. Dr Salisbury called attention to the very common association of Yew communities with steep slopes and suggested that the poverty of cover in these situations rendered them relatively immune from browsing animals (including rabbits) which often exhibit a partiality for Yew despite its poisonous effects. To this view Dr Watt agreed.

Mr Reginald Smith of the British Museum then made a statement with regard to a scheme which had been initiated on the Continent for mapping the distribution of Prehistoric Man. In this connection it was also desired to map the face of the Earth from Tertiary times to B.C. 0. He expressed the hope that the co-operation of the B.E.S. would be obtained in the mapping of the vegetation, and the President promised that the Council would consider the possibilities.

Prof. Fritch then gave an account of the encrusting Algae of swiftly flowing streams, as studied in North Devon. These consist of Cyanophyceae, chiefly species of *Phormidium*, a new species of *Oncobyrsa* which it was proposed to name *O. britannica*, the Red alga *Hildebrandtia rivularis* and a species of *Cocconeis*. A remarkable feature was the total absence or extreme rarity of Chlorophyceae. In the discussion which followed Mr Paulson drew attention to the frequency of certain lichens in such localities.

The last communication was from Prof. Oliver who gave an account of the formation and colonisation of Blakeney "Far Point." The vegetation is developed along lines which correspond to the position of buried zones of drift. The primary colonisers are *Triticum junceum*, *Psamma arenaria*, *Arenaria peploides* and the annuals *Cakile maritima* and *Salsola kali*. The processes of lateral spread, rise in height, and coalescence of the embryo dunes were dealt with, and emphasis was laid on the importance of storms in bringing aboutapid accretion and causing dense packing of the sand grains.

## LIST OF MEMBERS (10 JANUARY, 1925)

Corrections, omissions or changes of address should be notified at once to the *Hon. Secretary*, Dr E. J. SALISBURY, The Briars, Crosspath, Radlett, Herts.

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# STUDIES OF THE VEGETATION OF THE ENGLISH CHALK

## III. THE CHALK GRASSLANDS OF THE HAMPSHIRE-SUSSEX BORDER

BY A. G. TANSLEY AND R. S. ADAMSON.

(With Plates II-VI, and fifteen Figures in the Text.)

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### INTRODUCTION

The western end of the South Downs, in west Sussex, and just across the Hampshire border, nearly to the point where the chalk escarpment turns northward to form the western margin of the Weald, is very much more richly wooded than the central and eastern portions. This area in fact is one of the three larger existing areas of semi-natural English beechwood (*viz.* West Sussex, Chilterns and Thames valley, Cotswolds) and stretches, with few interruptions, from Arundel and Houghton in the Arun valley to Buriton and Ditcham Park

due south of Petersfield (which lies in the extreme south-western corner of the Weald), a distance of 18 miles (c. 29 km.)<sup>1</sup>.

Nevertheless considerable tracts of the chalk of this region are occupied by grassland alternating with the woods, though this grassland attains its greatest extent on and about the slopes of Butser Hill and War Down, where the London-Portsmouth road crosses the Downs, i.e. just beyond the western end of the woodland area referred to. Like most of the English chalk grassland it has been used as sheepwalk for centuries, though of recent years, especially since the war, there has been a tendency to replace sheep by cattle in many places. However the grassland may have originated there can be no doubt that the constant pasturing maintains it in its present condition. Rabbits (*Oryctolagus cuniculus*) are now locally very abundant (in some places indeed they are preserved, and even fed during the winter) and these eat the turf much closer than the sheep do, down to a height of less than an inch or even of a centimetre, and it is probable that the extreme shortness and "crispness" of the turf which delights the walker on the Downs is largely due to rabbits. Where the rabbit pressure is excessive these animals may, as we shall see, particularly in conjunction with moles (*Talpa europea*), destroy the grass turf altogether, especially on steep slopes, laying bare the chalk soil to the effects of rainwash down the slope. Under such conditions considerable areas become naked of vegetation or are tenanted only by individuals of certain species which the rabbits avoid. On the other hand, where cattle have replaced sheep, and rabbits are scarce or absent, the turf is much deeper, and species are present which cannot survive persistent rabbit nibbling or heavy sheep pasturing, probably because they depend on the possibility of fairly tall growth for success in maintaining themselves. In many places *Calluna vulgaris* and *Erica cinerea*, establishing themselves in the surface humous layers poor in lime, especially on the plateaux and gentler slopes, have lately increased considerably, apparently owing to this substitution of cattle for sheep. The cattle are not continuously pastured during the winter, and the heath plants are thus relieved of the continuous winter nibbling which is said to be specially destructive to them. In places which are not pastured at all tall meadow grasses appear on the chalk slopes with shallow soil, and with them, usually, the seedlings of woody species.

It is certain that much if not the whole of the chalk grassland would pass into forest if pasturing and rabbit attack were altogether stopped, as has been shown by the experiment of fencing against rabbits<sup>2</sup>.

<sup>1</sup> The beechwoods of this area have recently been dealt with pretty fully by one of us (R. S. Adamson, "The Woodlands of Ditcham Park, Hampshire"—the first publication in this series of "Studies," This JOURNAL, 9, pp. 114-219) and by Dr A. S. Watt ("On the ecology of British beechwoods with special reference to their regeneration," Part I, This JOURNAL, 11, pp. 1-48; Part II, *Ibid.* 12, pp. 145-204 and 13, pp. 27-73).

<sup>2</sup> Tansley, "Early Stages of redevelopment of Woody Vegetation on Chalk Grassland," Studies, II, This JOURNAL, 10, pp. 168-177.

The area considered in this paper extends from Butser Hill on the west to Downley Bottom on the east, a distance of 3 miles (4·8 km.), and from the north facing escarpment of the Lower Chalk southward to Windmill Hill and Chalton Down, a distance of a little over 3 miles (say 5 km.). The area lies almost entirely in Hampshire, the Sussex boundary crossing its eastern extremity (see Sketch-map, Fig. 1).

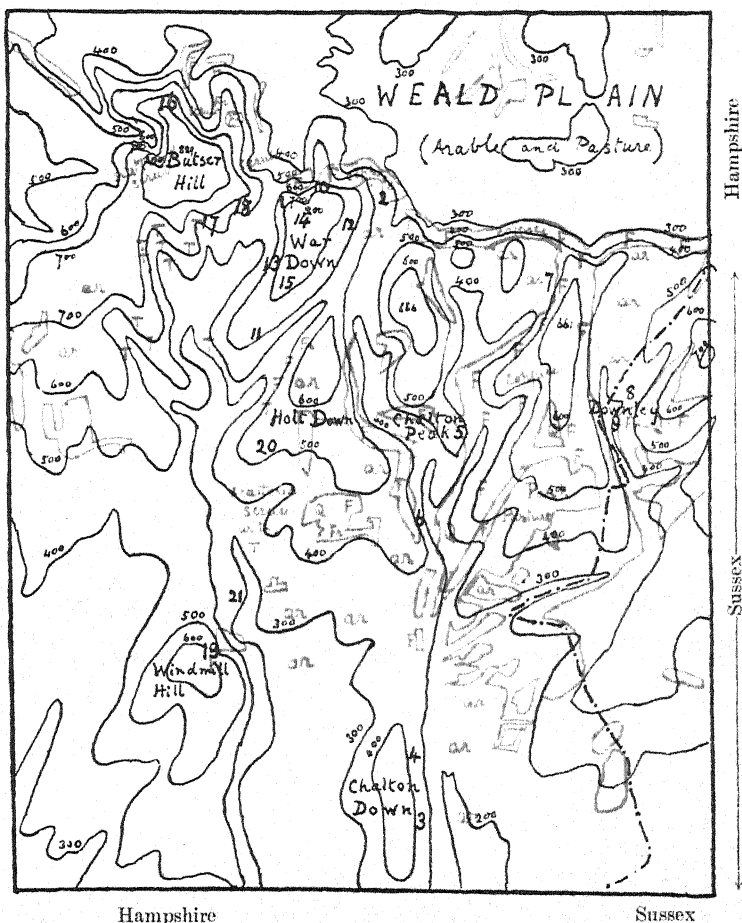


FIG. 1. Sketch-map of the region investigated. Scale 1 : 63,360. Railways, roads and villages omitted. Woods and plantations printed in red. Dominant trees F = *Fagus sylvatica*, Q = *Quercus robur*, Fr = *Fraxinus excelsior*, T = *Taxus baccata*, ar = arable land. Contour lines in feet (100 feet = 30·4 m.). The numbers 1-21 mark the areas described in the paper, where they are referred to by corresponding numbers in heavy type.

Owing to the fact that the denudation (i.e. the wearing down) of the surface of the chalk takes place by the solution of the calcium carbonate of which it mainly consists through the action of rain-water containing carbon dioxide, and not by mechanical disintegration as in the case of many "sili-



aceous" rocks, crags and precipitous faces of bare chalk rock are never met with except on the cliffs of the sea coast. The denudation proceeds slowly and continuously beneath the carpet of vegetation with which the rounded surfaces, whose slopes never exceed an angle of  $40^\circ$ , are clothed. By an examination of the sides and bottoms of chalk quarries, however, some information can be gained as to the earlier stages of the chalk succession.

## 1. SUCCESSION FROM BARE SURFACE TO GRASSLAND.

### A. COLONISATION OF BARE CHALK ROCK.

Almost the only plant actually met with establishing itself on the bare surface of blocks of chalk, whether *in situ* or detached, was the moss *Seligeria calcarea*. This however we found to be abundant, for instance at the upper quarry at Buriton Limeworks, its embedded protonema turning grey the surfaces of blocks which had been exposed for some time. Fruiting specimens were also rather frequent. Associated with it was occasionally an alga (*Chroolepus* sp.), but no lichens were discovered here. This colonisation cannot be regarded as forming part of the developmental series leading to chalk grassland. Events would doubtless follow the same course if the alga and moss were absent.

A certain number of flowering plants are able to settle among the fine chalk particles along the bedding planes and joints of an irregularly inclined quarry side which presents slopes at various angles. In such a situation we found at Buriton upper quarry the following:

<i>Crepis capillaris</i>	<i>Linaria minor</i>
<i>Dactylis glomerata</i>	<i>Senecio vulgaris</i>
<i>Epilobium montanum</i>	<i>Taraxacum erythrospermum</i>
<i>Koeleria gracilis</i>	<i>T. officinale</i>
<i>Leontodon hispidus</i>	<i>Thymus serpyllum</i>

On a roadside chalk cutting, sloping at an angle of  $45^\circ$ , were isolated plants of *Echium vulgare*, *Festuca ovina*, *Senecio jacobaea* and *Tussilago farfara*. Maritime cliffs would no doubt yield a greater variety of species, rooted, like all the above, in the joints and fissures and along the bedding planes of the bare chalk rock.

As a direct result of quarrying operations, and also of the falling and disintegration of lumps of chalk detached from the sides of the quarries through rainwater penetrating along the joints and bedding planes and thus isolating blocks of the rock, a talus of chalk fragments of various sizes, showing a maximum slope of  $38^\circ$ – $40^\circ$ , frequently accumulates at the foot of the vertical quarry face, and these are rapidly reduced in size by solution and disintegration and give rise to a substratum easily colonised by flowering plants.

### B. COLONISATION OF CHALK TALUS AND SPOIL SURFACES.

The natural and artificial quarry talus, which rests at an angle of  $38^\circ$ – $40^\circ$ , consists of angular pieces of chalk of very various sizes. The largest may be 12 or 15 inches long, but the majority do not exceed 2 to 4 inches (5–10 cm.)

in diameter, and these are mixed with small to tiny fragments among which flowering plants can establish themselves. The larger lumps, like the surface of the living rock, may be colonised by *Seligeria calcarea*.

A series of talus slopes and spoil banks in abandoned quarries at the western foot of War Down (1)<sup>1</sup>, near the Portsmouth road, gave an excellent series illustrating the development of vegetation on such surfaces. A clear distinction could be drawn between the colonists of fairly coarse talus and those of the slopes consisting of finer particles. On the former *Senecio jacobaea* and *Echium vulgare* were predominant, on the latter *Tussilago farfara* and *Festuca ovina*.

The following lists are taken from three slopes of the fine spoil banks in these quarries:

Table I.

(1) is a S-facing slope with about 60 per cent. of bare chalk "soil." *Festuca ovina* is the leading colonist, with *Carex flacca* next;

(2) the N-facing slope of the same bank with about 40 per cent. of the surface bare. Here *Festuca* and *Tussilago* are predominant;

(3) the S-facing slope of another bank in a more advanced stage with only about 10 per cent. of bare surface. *Festuca ovina* and *Carex flacca* are co-dominant and *Echium* is prominent.

	1	2	3		1	2	3
<i>Achillea millefolium</i>	—	—	o.	<i>Myosotis arvensis</i>	—	r.	—
<i>Agrostis alba</i>	f.—a.	a.—f.	a.	<i>Ophrys apifera</i>	—	—	l.
<i>Anthoxanthum odoratum</i>	f.	r.	f.	<i>Plantago lanceolata</i>	—	—	o.
<i>Arrhenatherum elatius</i>	—	o.l.	—	<i>Ranunculus bulbosus</i>	—	—	f.
<i>Asperula cynanchica</i>	o.	—	o.	<i>Rosa canina</i>	—	—	r.
<i>Avena pratensis</i>	o.	o.	o.	<i>Senecio jacobaea</i>	—	o.	o.
<i>Bellis perennis</i>	—	—	o.	<i>Sonchus oleraceus</i>	o.	—	—
<i>Campanula rotundifolia</i>	—	—	o.	<i>Taraxacum erythrospermum</i>	o.	—	—
<i>Carex caryophylla</i>	—	—	l.	<i>T. officinale</i>	f.	f.	o.
<i>C. flacca</i>	l.a.	l.	c.d.	<i>Thymus serpyllum</i>	f.	l.a.	f.
<i>Carlina vulgaris</i>	f.	o.	o.	<i>Tussilago farfara</i>	l.d.	a.l.d.	—
<i>Cirsium acule</i>	l.f.	o.	v.a.	MOSSES			
<i>C. palustre</i>	o.	—	—	<i>Barbula rigidula*</i>	—	—	o.
<i>Clematis vitalba</i>	r.	—	—	<i>Brachythecium purum</i>	—	—	l.a.
<i>Cynoglossum officinale</i>	—	r.	—	<i>Camptothecium lutescens*</i>	f.	f.—a.	v.a.
<i>Dactylis glomerata</i>	o.	l.	l.	<i>Fissidens taxifolius</i>	—	—	l.a.
<i>Echium vulgare</i>	l.f.	—	o.—f.	<i>Hypnum chrysophyllum*</i>	o.	l.f.	—
<i>Euphrasia nemorosa</i>	o.	—	—	<i>H. cuspidatum</i>	—	o.	o.
<i>Festuca ovina</i>	v.a.	v.a.	c.d.	<i>H. molluscum*</i>	f.	l.a.	f.
<i>Gentiana amarella</i>	l.a.	—	—	<i>Neckera complanata</i>	o.	—	—
<i>Hieracium pilosella</i>	f.	o.	o.	<i>N. crispa*</i>	—	—	l.
<i>Leontodon hispidus</i>	o	o.	f.—a.	<i>Thuidium abietinum</i>	—	—	a.
<i>Linum catharticum</i>	f.	f.	o.—f.				
<i>Lotus corniculatus</i>	a.	f.	f.	Total number of species	27	23	33

\* Given by Watson as "calcicole" species.

If these lists are compared, it is seen that *Cynoglossum officinale*, *Sonchus oleraceus* and *Tussilago farfara* (plants of "waste places" and open soil generally) occur only in the less advanced stages (1) and (2), while (3), where the vegetation is nearly closed, has several more species characteristic of chalk grassland and not found in the other two lists. But some of the colonisation is clearly a matter of chance. Of the mosses three out of the four

<sup>1</sup> The figures in heavy type throughout the paper refer to the localities, correspondingly numbered on the sketch-map (Fig. 1, p. 179), in which the various studies were made.

occurring in (1), and four out of the eight occurring in (3) are given by Watson as "calicicole" species<sup>1</sup>. *Brachythecium purum*, an abundant and constant moss of chalk grassland, though not a "calicicole," becomes locally abundant in (3), together with *Fissidens taxifolius* and *Thuidium abietinum*, which are also species "indifferent" as regards lime in the habitat, according to Watson.

The lists clearly represent stages in the short subseres leading back to chalk grassland.

SOILS of (1) Top inch	Water-loss of air-dry soil at 100° C.	Loss on ignition (mainly organic matter)	Total carbonates (as CaCO <sub>3</sub> )	CaO	MgO	K <sub>2</sub> O	Insol. residue	pH
(1) <i>Festuca ovina</i> freshly colonised	1.1	3.03	90.5	49.26	0.22	0.08	5.3	8.0?
(2) Greyer soil under older fescue tufts	1.5	5.18	86.1	49.7	0.29	0.09	5.2	8.0?

The sides and bottom of the upper quarry above Buriton at Buriton Limeworks (2), which is still worked but is largely occupied by vegetation on the faces not actually being quarried, present a much larger and more varied list of species. This is doubtless because this quarry is much closer to both arable land and woodland than is the case with the old War Down quarries, which are surrounded by great stretches of chalk grassland. Seeds and fruits are no doubt also constantly brought in by the traffic to the quarry.

The following plants were found among the chalk talus on the sides of the quarry:

<i>Agrostis alba</i>	<i>Reseda luteola</i>
<i>Acer pseudoplatanus</i>	<i>Rubus rusticanus</i>
<i>Clematis vitalba</i>	<i>Salix caprea</i>
<i>Crataegus monogyna</i>	<i>Senecio jacobaea</i>
<i>Epilobium angustifolium</i>	<i>Solanum dulcamara</i>
<i>Galeopsis ladanum</i>	<i>Sonchus arvensis</i>
<i>Origanum vulgare</i>	<i>Sorbus aria</i>
<i>Pastinaca sativa</i>	<i>Tussilago farfara</i>
<i>Plantago lanceolata</i>	<i>Verbascum nigrum</i>
<i>Poa annua</i> (on fine talus)	

All but four of these 19 species were also present on the floor of the quarry (see list below).

On one part of the floor of the quarry was a horizontal stretch of bare chalk whose surface had apparently been cemented by partial solution and drying, and was cracking in places. This surface was rather more than half covered with vegetation of sorts, but the great bulk of it consisted solely of the protonema of *Seligeria calcarea*\*. Perhaps 10 per cent. of the surface was occupied by the following mosses:

<i>Barbula cylindrica</i> * a.	<i>Camptothecium lutescens</i> * r.	<i>Lophozia turbinata</i> * l.a.
<i>B. unguiculata</i> o.	<i>Dicranella varia</i> l.a.	<i>Seligeria calcarea</i> * f.
<i>Bryum argenteum</i> f.	<i>Funaria hygrometrica</i> l.	(fruiting on chalk lumps)

\* Calicicole according to Watson.

The flowering plants, which probably did not occupy 1 per cent. of the whole surface, were the following:

<sup>1</sup> W. Watson. "The Bryophytes and Lichens of Calcareous Soil." This JOURNAL, 6, pp. 189-198.

<i>Acer pseudoplatanus</i> (one seedling)	—	<i>Euphrasia nemorosa</i>	o.	<i>Poa annua</i>	a.
<i>Agrostis alba</i> (creeping and rooting at the nodes—spreading)	f.	<i>Festuca ovina</i>	o.—f.	<i>Poterium sanguisorba</i>	r.
<i>Anthoxanthum odoratum</i>	r.	<i>F. rigida</i>	o.	<i>Prunella vulgaris</i>	o.
<i>Arenaria serpyllifolia</i>	o.	<i>Fragaria vesca</i>	r.	<i>Ranunculus repens</i>	o.
<i>Avena pratensis</i>	o.	<i>Galeopsis ladanum</i>	r.	<i>Reseda luteola</i>	o.
<i>Campanula rotundifolia</i>	r.	<i>Galium verum</i>	o.	<i>Rumex acetosella</i>	r.*
<i>Carduus nutans</i>	r.	<i>Hieracium pilosella</i>	r.	<i>R. crispus</i>	l.
<i>Carex flacca</i>	o.	<i>Holcus lanatus</i>	o.	<i>Sagina procumbens</i>	o.
<i>Centaurea nigra</i>	o.	<i>Leontodon autumnalis</i> (confined to tufts of <i>Agrostis alba</i> )	l.	<i>Salix caprea</i> (one seedling)	l.f.
<i>Cerastium vulgatum</i>	o.	<i>L. hispidus</i>	o.	<i>Senecio jacobaea</i>	l.f.
<i>Cirsium acaule</i>	r.	<i>Linaria minor</i>	f.	<i>S. vulgaris</i>	r.
<i>C. lanceolatum</i>	r.	<i>Linum catharticum</i>	o.	<i>Sisymbrium alliaria</i>	r.
<i>Clematis vitalba</i>	r.	<i>Lotus corniculatus</i>	r.	<i>Sonchus asper</i>	o.
<i>Crepis capillaris</i>	l.f.	<i>Matricaria inodora</i> (many seedlings)	o.	<i>Taraxacum erythrospermum</i>	o.
<i>Cucubalus behen</i> ( <i>Silene inflata</i> )	r.	<i>Medicago lupulina</i>	o.	<i>Thymus serpyllum</i>	l.
<i>Daactylis glomerata</i>	o.	<i>Myosotis arvensis</i>	o.	<i>Trifolium pratense</i>	r.
<i>Epilobium angustifolium</i>	l.	<i>Origanum vulgare</i>	l.	<i>T. repens</i>	l.f.
<i>E. montanum</i>	o.	<i>Pastinaca sativa</i>	f.	<i>Urtica dioica</i>	r.
		<i>Plantago lanceolata</i>	o.	<i>Verbascum nigrum</i>	o.
		<i>P. major</i>	o.—f.	<i>Veronica arvensis</i>	r.
				<i>V. serpyllifolia</i>	r.

\* A remarkable occurrence on pure chalk.

This miscellaneous assortment of 60 species is to be accounted for by the proximity of the area to woodland and arable land as well as to chalk grassland, and by the fact that the surface is somewhat trampled, which would probably help to bring in weeds. The mixed "community" clearly does not stand in a normal line of succession, but is of interest as showing the large number of varied species which can colonise such a habitat.

## 2. CHALK GRASSLAND.

### A. AT BURITON LIMEWORKS.

The small area of chalk grassland existing round Buriton Limeworks (2) is of interest because it appears to represent "primitive" chalk grassland, i.e. grassland with characteristic associated herbs developed on a shallow chalk soil and practically unaffected by pasturing or rabbit attack, more nearly than any other area in the region dealt with<sup>1</sup>. It is impossible to say exactly how old the vegetation of this particular area of chalk grassland is. The area, whose surface is somewhat irregular, was probably bared at some stage in the development of the quarries, but unlike the quarry still being worked, from which lists were given in Section 1, it has been completely colonised by the grassland community, which now forms a closed turf, except on the south-facing slope of a hillock where the soil is shallowest and driest (see (a) below), and even here the turf is practically closed. Thus it represents a later stage of development than the spoil slopes of the quarry at the foot of War Down dealt with in Section 1, though still an early stage.

Three small patches, each of about 2 square metres, and in close proximity, are compared. They show progressive increase in height and density of vegetation, with an increasing number of species, correlated with increasing water, humus, and nitrate content, and slightly decreasing carbonate content of the soil.

<sup>1</sup> On one visit a little local rabbit dung was found on the area.

Table II. *Vegetation and soils of three small areas of "primitive" chalk grassland in close proximity.*

(a) Turf scarcely continuous. Herbage  $\frac{1}{2}$ –1 inch (1.25–2.5 cm.) in height. Slope to S.S.W. 18°–20°. Soil  $2\frac{1}{2}$ –3 inches (6.25–7.5 cm.) in depth to chalk *in situ*, grey, very dry and powdery, included in a mass of fine rootlets.

(b) Turf more continuous. Herbage 4 inches (10 cm.) in height. Very slight slope to south. Soil 4 inches (10 cm.) in depth to chalk *in situ*, grey-brown.

(c) Close herbage 5 inches (12.5 cm.) in height. Bottom between two hummocks. Soil 4 inches (10 cm.) to chalk *in situ*, brown.

	Soil samples	Water loss of fresh soil on air drying	Water loss of dry soil at 100° C.	Loss on ignition	Total carbonates	Nitrates as NaNO <sub>3</sub>	P <sub>2</sub> O <sub>5</sub>	K <sub>2</sub> O	MgO	CaO	Insol. residue	"Lime requirement"
(a)	D 8	17.0	3.0	6.2	71.1	.0048	.160	.327	.201	54.6	14.6	Nil
(b)	D 9	27.0	4.0	19.7	65.9	.0037	.164	.640	.183	32.1	5.6	Nil
(c)	D 10	33.8	4.6	28.6	62.8	.0500	.170	.301	.062	36.25	22.0	Nil

	(a)	(b)	(c)		(a)	(b)	(c)
Agrostis alba	—	f.	a.	Plantago lanceolata	r.	o.	f.
Asperula cynanchica	f.	a.	f.	Primula veris	—	—	r.
Avena pratensis	r.	—	o.	Ranunculus bulbosus	o.	o.	o.
Bellis perennis	—	o.	—	Taraxacum erythrospermum	o.	—	—
Briza media	o.	o.	o.	Thymus serpyllum	f.	a.	f.
Campanula rotundifolia	o.	f.	o.	Trifolium pratense	o.	f.	f.—a.
Centaurea nigra	r.	f.	o.	T. repens	—	o.	o.
Cynosurus cristatus	—	f.	a.	Trisetum flavescens	o.	a.	a.
Dactylis glomerata	—	—	f.—l.a.				
Euphrasia nemorosa	—	—	o.	Barbula cylindrica*	a.	f.	—
Festuca ovina	d.	v.a.	a.	B. unguiculata	o.	—	—
Galium verum	—	f.	o.	Brachythecium purum	—	o.	f.
Hieracium pilosella	f.l.a.	a.	f.	B. rutabulum	—	—	o.
Holcus lanatus	—	—	f.	Bryum capillare	o.	—	—
Leontodon hispidus	f.	f.	f.	Camptothecium lutescens*	f.	—	o.
Linum catharticum	o.	—	o.	Fissidens taxifolius	o.	o.	—
Lolium perenne	—	o.	—	Hypnum cuspidatum	—	—	o.
Lotus corniculatus	f.	a.	f.	H. molluscum*	o.	f.	—
Medicago lupulina	f.	a.	f.	Mnium undulatum	—	—	o.
Origanum vulgare	—	—	r.	Thuidium abietinum	a.	o.	—
Phleum pratense	—	—	—	T. tamariscinum	—	—	o.
var. nodosum	f.	—	—				
				Total	25	25	31

A comparison of the three soils shows a steady increase from (a) to (c) in water content and in humus and a decrease in total carbonates and in calcium. The nitrate determinations, made some four months after the samples were collected, are probably rather an index of the abundance of nitrifying or nitrogen fixing organisms in (c) than a trustworthy measure of the amount of nitrates in the soil as it exists in the field.

The characteristic feature of the vegetation of (a) is its extreme dwarfing, due no doubt primarily to drought. The shallow rooting *Festuca ovina* is markedly dominant, forming more than half of the whole herbage. The other grasses are few (four species) and not abundant. The rest of the vegetation is made up of a small selection of the common herbs of dry grassland, of which *Hieracium pilosella*, *Leontodon hispidus*, *Lotus corniculatus*, *Thymus serpyllum* and *Asperula cynanchica* were most conspicuous. Of these the last named is the only one which is practically confined to chalk and other limestones in this country. The only two species found on this area and not on (b) or (c)

are *Taraxacum erythrospermum* and *Phleum pratense* var. *nodosum*, both plants of markedly dry soils. Of the seven mosses four are distinctly xerophilous forms, and three are marked by Watson as calcicole<sup>1</sup>.

Comparing (b) and (c) with (a) there is an increase in the number of species of grass from 5 to 6 and 8 respectively, and in (c) a great increase in the bulk of grass herbage. This is to be correlated with the great increase in water content and the much greater nitrifying power of the soil of (c). *Agrostis alba*, *Cynosurus cristatus*, *Dactylis glomerata*, *Lolium perenne* and *Holcus lanatus* appear, *Trisetum flavescens* increases in abundance, while *Festuca ovina* progressively decreases, though it still remains abundant. Of the herbs *Trifolium repens* appears, *T. pratense* and *Plantago lanceolata* increase in abundance, while some species, such as *Asperula cynanchica*, *Campanula rotundifolia*, *Hieracium pilosella*, *Lotus corniculatus* and *Thymus serpyllum* show their maximum frequency in (b), perhaps owing to the competition of the taller grasses in (c). *Euphrasia nemorosa*, *Origanum vulgare* and *Primula veris* appear for the first time in (c).

Of the mosses, *Barbula cylindrica*, *B. unguiculata* and *Bryum capillare* decrease and disappear with complete closure and increasing depth of the turf; *Brachythecium purum*, one of the most ubiquitous of chalk grassland mosses, though not a "calcicole" species, appears in (b) and increases in (c); while *B. rutabulum*, *Mnium undulatum* and *Thuidium tamariscinum* first appear in the damper conditions of (c).

The following is a general list of species from the Buriton Lineworks chalk grassland. The arable and wayside weeds, woodedge and dry bank herbs, which have invaded this grassland area, but are never more than rare, are in italics:

Achillea millefolium	o.	Hieracium pilosella	l.a.	Scabiosa columbaria	l.a.
Agrostis alba	o.	Holcus lanatus	l.a.	Senecio jacobaea	o.
Anthraxanthum odoratum	l.	Koeleria gracilis (eristata)	o.	Taraxacum erythrospermum	o.
Asperula cynanchica	f.	Leontodon autumnalis	o.	Thymus serpyllum	a.
Avena pratensis	f.	L. hispidus	f.	Trifolium pratense	a.
Bellis perennis	o.	Linum catharticum	f.	T. repens	r.—o.
Briza media	f.	Lolium perenne	r.	Trisetum flavescens	a.
Campanula rotundifolia	f.	Lotus corniculatus	a.	Tussilago farfara	r.
Carex flacca	a.	Matricaria inodora	r.	Urtica dioica	r.
Carlina vulgaris	o.	Medicago lupulina	a.	Verbascum nigrum	r.
Centaurea nigra	o.	Orehis pyramidalis	r.	V. thapsus	r.
Cerastium vulgatum	r.	Origanum vulgare	r.	Veronica arvensis	r.
Cirsium acaule	f.—l.a.	Pastinaca sativa	r.	V. chamaedrys	l.
C. arvense	r.	Phleum pratense var.	lf.		
Clinopodium vulgare	r.	nodosum		WOODY PLANTS	
Crepis virens	r.	Pimpinella saxifraga	o.	Clematis vitalba	r.
Cynosurus cristatus	f.—a.	Plantago lanceolata	o.	Cornus sanguinea	r.
Dactylis glomerata	r.	P. media	f.	Crataegus monogyna	o.
Euphrasia brevipila	o.	Potentilla anserina	r.	Quercus robur (seedling)	r.
E. nemorosa	f.	P. reptans	r.	Rosa canina (agg.)	r.
Festuca ovina	v.a.	Poterium sanguisorba	l.	R. micrantha	r.
Galium erectum	l.	Primula veris	r	R. rubiginosa	r.
G. mollugo	r.	Prunella vulgaris	o.	Rubus caesius	r.
G. verum	a.	Ranunculus bulbosus	o.	R. rusticanus	r.
Gentiana amarella	o.	Rumex crispus	r.		
Heracleum sphondylium	r.	R. obtusifolius	r.		

<sup>1</sup> W. Watson. "The Bryophytes and Lichens of Calcareous Soil." This JOURNAL, 6, 1918.

BRYOPHYTES					
<i>Urbula cylindrica</i> *	o.l.	<i>Fissidens adiantoides</i>	o.	<i>Seligeria calcarea</i> (chalk lumps only)*	l.
<i>fallax</i>	o.	<i>F. taxifolius</i>	o.	<i>Thuidium abietinum</i>	l.a.
<i>rubella</i>	r.	<i>Hylocomium splendens</i>	f.—l.a.	<i>T. tamarascinum</i>	l.f.
<i>unguiculata</i>	o.	<i>H. squarrosum</i>	o.—l.f.	<i>Webera carnea</i>	r.
<i>Cachypthecium purum</i>	f.	<i>Hypnum cupressiforme</i>	o.—f.		
<i>rutabulum</i>	o.	<i>var. resupinatum</i>			
<i>Cyrum capillare</i>	o.	<i>H. cuspidatum</i>	o.	<i>Lophocolea bidentata</i>	o.
<i>Amptothecium lutescens</i> *	a.	<i>H. molluscum</i> *	a.	<i>Lophozia turbinata</i> *	l.a.
		<i>Mnium undulatum</i>	r.	<i>Pellia calycina</i>	l.
		<i>Neckera crispa</i> *	l.a.		

\* Calicicole species.

## B. CHALTON DOWN AND CHALTON PEAK.

Two areas (3 and 4) of an acre or so on the former, and one on the latter (5), were listed (Table III, first three columns). The three are comparable examples of fairly typical and uniform chalk grassland. They are all situated on the same chalk ridge, and have an eastern exposure and a moderate to fairly steep slope (24°–32°—the steepest local slope measured was 35°). They were all pastured by sheep, but not heavily, and there was no noticeable rabbit pressure. The general height of the herbage in (3) and (5) was 2–3 inches (5–7.5 cm.). The depth of the soil was fairly uniform in the southern area (3), averaging 4 inches to the layer of large chalk lumps, with soil between, which extended downwards for another 4 inches to the fissured upper surface of the rock. In the northern area (4) of Chalton Down, towards the bottom of the slope, at 17°, 10 inches of brown loam were present before any considerable chalk lumps occurred. Chemical analysis gave the following results:

Depth of sample	Water loss of air dry soil at 100° C.	Loss on ignition	Total carbonates (as CaCO <sub>3</sub> )	Nitrates (as NaNO <sub>3</sub> )	P <sub>2</sub> O <sub>5</sub>	K <sub>2</sub> O	MgO	CaO	Insol. residue	"Lime requirement" pH
3. Top inch (slope 24°)	10.1	24.35	1.8	.0086	.287	.204	.197	.41	36.5	.09
1"–4" (slope 24°)	5.45	17.46	28.6	—	—	.180	.165	17.4	29.0	—
4. 4"–9" (slope 17°)	4.0	11.56	30.2	—	—	.116	.46	18.0	29.8	—

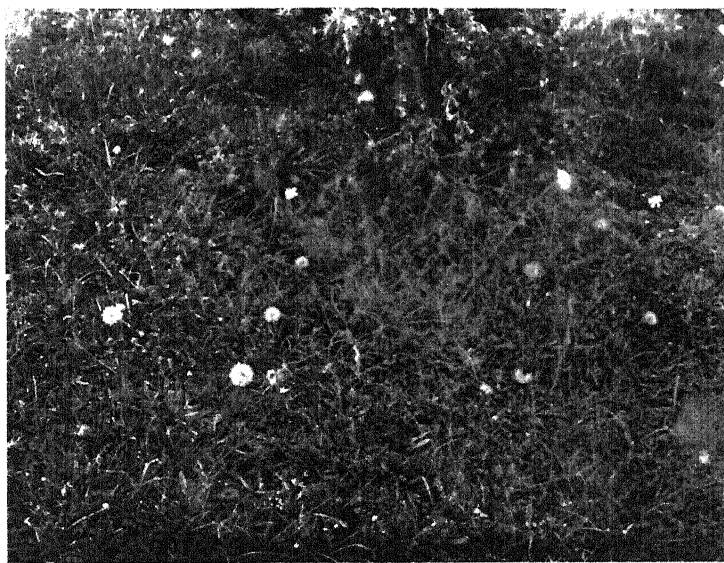
showing the characteristic poverty in lime of the surface layer of typical chalk grassland soil.

The southern part of Chalton Down (3) is dotted with single bushes and clumps of *Juniperus communis* (Pl. II, Fig. 1), ranging from 3 feet (nearly 1 metre) to 10 feet (3 m.) in height<sup>1</sup>, and seedling junipers are scattered in the grassland. But these do not affect the intervening herbage. The northern part (4) has fewer junipers and is less pastured, so that the grasses grow more luxuriantly. Chalton Peak (5) is similar but closer to continuous areas of woodland. In all three areas *Festuca ovina* is the most abundant grass, but in none does it form quite half the bulk of the herbage. The lists given below were obtained by repeated careful traverses of the areas in all directions, and the usual frequency letters are appended. As a check on the subjective estimates of frequencies, the species present in 50 quadrats of one square foot (about 9.3 square decimeters) all taken at random in the southern Chalton Down area

<sup>1</sup> There appear to be two distinct (? hereditary) growth forms of *Juniperus communis*: one is low growing and often flat-topped, the other has a strict pyramidal habit recalling *Cupressus sempervirens* var. *pyramidalis*, or the "Irish Yew." These are not "habitat forms" since they often grow side by side.



Phot. 1. Chalton Down (South), east slope, typical chalk grassland, moderately pastured, with scattered juniper bushes (and seedlings).



Phot. 2. Detail of phot. 1. Base of juniper bush at back. Several plants of *Leontodon hispidus* in fruit (pappus). *Galium verum* in centre. Other plants visible include *Festuca ovina*, *Carex flacca*, *Cirsium acaule*, *Poterium sanguisorba*, *Scabiosa columbaria* and *arvensis*, *Spiranthes autumnalis*.





were noted. There was an average occurrence of between 16 and 17 species on each square foot sampled. The numbers so obtained were doubled so as to express percentage frequencies on the sampled area. These are given in the first column (3) following the frequency letters. The result shows that the correspondence is far from exact. The species noted as "abundant" occurred in 34 to 100 per cent. of the 1-foot quadrats, all but one occurred in over 55 per cent. and all but two in over 75 per cent. The mean percentage occurrence of the "abundant" species is 81. At the other extreme

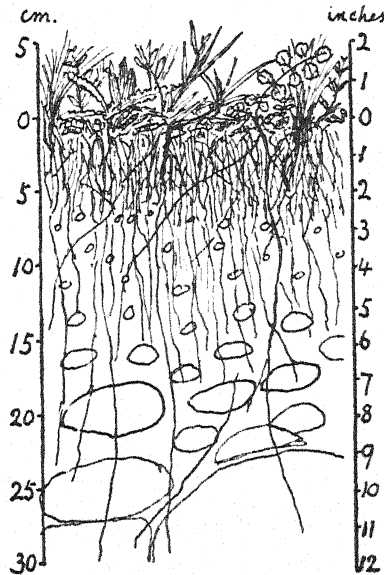


FIG. 2. Chalton Peak (5), profile of herbage and soil, August, 1914, somewhat diagrammatic. Soil 0-7 cm. firmly held by roots of *Festuca ovina*, *Arena pratensis* and *pubescens*, *Hieracium pilosella*, *Linum catharticum*, *Leontodon hispidus*, *Ranunculus bulbosus*, *Plantago lanceolata* and most of the root systems of *Carex flacca*; 7-15 cm. soil with small fragments of chalk up to 1 cm. in diameter lightly held by root systems of *Asperula cynanchica*, *Thymus serpyllum*, *Trifolium pratense* and some *Carex flacca*; 15-25 cm. loose soil with roots of *Poterium sanguisorba*, *Cirsium acule* and some *Lotus corniculatus*, and numerous lumps of chalk (with a very few flints) increasing in size downwards and passing to fissured chalk *in situ* with soil in the fissures into which the longest roots pass.

none of the "rare" species occurred in any of the sample quadrats. These are the most satisfactory correspondences. The percentage range of the "occasional" species is 0-24, and the mean occurrence 7.8 per cent., if we omit *Linum catharticum* which is marked as "occasional" though it occurs in 82 per cent. of the quadrats. This species is decidedly inconspicuous when not in flower and there can be no doubt that it was extensively overlooked in the traverses and should have been marked as "abundant." The "frequent" species range from 2 to 88 per cent. with a mean of 28. More quantitative checks of this kind are needed after the subjective estimations have been made with all possible care.



In addition to the few woody species found as seedlings or isolated bushes scattered over the grassland areas 3-5, and included in the list, there was a small vestigial belt of scrubby woodland at one end of (3) and in the immediate neighbourhood of this there occurred, in addition, *Corylus avellana*, *Fagus sylvatica* (seedlings), *Hedera helix*, *Ilex aquifolium*, *Lonicera periclymenum*, *Quercus robur*, *Rosa arvensis*, *Rubus rusticanus*, *Sambucus nigra*, *Sorbus aria*, and *Taxus baccata*. Most of the casuals and woodland plants printed in italics in the list were found in this vicinity.

#### C. COULTER'S DEAN "WASTELAND" (7).

This is a strip of "waste" land, little if at all pastured, about a quarter of a mile (400 m.) long and less than 100 yards broad, bounded on one side (east) by beechwood and on the other (west) by arable land. It has a very slight slope to the west. It is occupied by a mixture of grasses, dicotyledonous herbs and woody plants (shrubs and young trees) and is of interest mainly because two lists are available, one made in 1914 and the other, quite independently, in 1920. From a comparison of these it will be seen that the number of species is recorded as having increased from 85 to 107 and that 32 species, including six of the woody ones, increased in frequency, while four species disappeared and nine appear to have decreased in frequency. Of course a considerable margin of error, both in missing species that were present and in wrongly estimating frequencies, must be allowed for, but the figures are nevertheless quite sufficient to show that there was an increase both in species and individuals during the six years. Clearly the area represents a stage in succession of derelict arable, which is marked by the mixture of plants referred to above. Pastured it would doubtless become chalk grassland with fair rapidity. Left to itself it would revert to woodland. This is in accordance with the view, supported by other facts given in this paper, that chalk grassland is essentially a "subclimax" community stabilised by pasturing.

Table IV. *Flora of Coulter's Dean wasteland (7).*

	1914	1920		1914	1920
<i>Agrimonia eupatorium</i>	o.	l.o.	<i>C. scabiosa</i>	o.	l.f.
<i>Agropyrum repens</i>	—	r.	<i>Cirsium arvense</i>	—	r.
<i>Agrostis tenuis</i> and <i>alba</i>	o.	o.	<i>C. acule</i>	o.	o.
<i>Anthoxanthum odoratum</i>	—	o.	<i>Clinopodium vulgare</i>	o.	l.f.
<i>Anthyllis vulneraria</i>	o.	o.—l.f.	<i>Conopodium majus</i>	r.	—
<i>Arenaria serpyllifolia</i>	—	r.	<i>Cucubalus behen</i> ( <i>Silene inflata</i> )	o.	l.
<i>Arrhenatherum elatius</i>	l.	l.a.—l.d.	<i>Cynosurus cristatus</i>	r.	—
<i>Asperula cynanchica</i>	o.	o.	<i>Dactylis glomerata</i>	f.	f.
<i>Avena pratensis</i>	l.	o.	<i>Daucus carota</i>	o.	o.
<i>A. pubescens</i>	o.	o.	<i>Epipactis latifolia</i>	l.	—
<i>Bellis perennis</i>	r.	—	<i>Erythraea centaurium</i>	o.	o.
<i>Blackstonia perfoliata</i>	l.o.	l.o.	<i>Euphrasia nemorosa</i>	o.	o.
<i>Brachypodium silvaticum</i>	a.	a.—l.d.	<i>Festuca ovina</i>	l.a.	l.
<i>Briza media</i>	f.	f.	<i>Fragaria vesca</i>	o.	l.a.
<i>Calamintha acinos</i>	r.	o.	<i>Galeopsis ladanum</i>	—	r.
<i>Campanula glomerata</i>	o.	f.	<i>Galium erectum</i>	o.	f.
<i>C. rotundifolia</i>	—	l.	<i>G. mollugo</i>	—	f.
<i>Carex flacca</i> (glauca)	a.	a.	<i>Gentiana amarella</i>	o.	l.f.
<i>Carlina vulgaris</i>	o.	o.	<i>Geranium columbinum</i>	—	r.
<i>Centaurea nigra</i>	o.	l.a.	<i>Habenaria chlorantha</i>	—	r.

Table IV (continued).

	1914	1920		1914	1920
<i>H. conopsea</i>	r.	r.	<i>Veronica chamaedrys</i>	r.	—
<i>Helianthemum vulgare</i>	o.	l.	<i>Vicia cracca</i>	o.	o.
<i>Heracleum sphondylium</i>	r.	o.	<i>V. hirsuta</i>	r.	r.
<i>Hieracium pilosella</i>	l.a.	l.a.	<i>Viola hirta</i>	l.	l.a.
<i>Holcus lanatus</i>	o.	o.		Total 66	81
<i>Hypericum hirsutum</i>	—	o.			
<i>H. perforatum</i>	o.	f.	WOODY PLANTS		
<i>Leontodon hispidus</i>	—	v.a.	<i>Betula alba</i>	—	l.
<i>Leucanthemum vulgare</i>	o.	o.—f.	<i>Clematis vitalba</i>	r.	o.
<i>Linum catharticum</i>	f.	f.—a.	<i>Cornus sanguinea</i>	o.	o.
<i>Lotus corniculatus</i>	a.	a.	<i>Corylus avellana</i>	o.	o.
<i>Medicago lupulina</i>	o.	f.	<i>Crataegus monogyna</i>	o.	o.
<i>Ononis repens</i>	o.	l.a.	<i>Fagus silvatica</i>	r.	r.—o.
<i>Ophrys apifera</i>	o.	r.	<i>Fraxinus excelsior</i>	r.	—
<i>Orchis maculata</i>	o.	o.	<i>Prunus spinosa</i>	o.	o.—l.d
<i>O. pyramidalis</i>	—	o.	<i>Pyrus malus</i>	—	r.
<i>Origanum vulgare</i>	f.	a.	<i>Quercus robur</i>	r.	r.
<i>Pastinaca sativa</i>	o.	l.	<i>Rhamnus catharticus</i>	—	r.
<i>Phleum pratense</i>	—	r.	<i>Rosa arvensis</i>	—	o.
<i>Pimpinella saxifraga</i>	l.a.	o.—f.	<i>R. canina</i>	r.	r.
<i>Plantago lanceolata</i>	o.	f.	<i>R. micrantha</i>	—	r.
<i>Poa trivialis</i>	—	r.	<i>R. rubiginosa</i>	r.	r.
<i>Polygala vulgaris</i>	o.	o.	<i>Rubus coesius</i>	f.	l.a.
<i>Potentilla reptans</i>	—	o.	<i>R. rusticanus</i>	—	l.
<i>Poterium sanguisorba</i>	a.	a.	<i>Salix caprea</i>	o.l.	o.l.
<i>Primula veris</i>	l.	l.	<i>Sorbus aria</i>	r.	o.
<i>Prunella vulgaris</i>	o.	f.	<i>Viburnum lantana</i>	r.	o.
<i>Rumex crispus</i>	—	r.		Total 14	19
<i>Sanicula europaea</i>	—	r.			
<i>Scabiosa arvensis</i>	f.	f.	MOSSSES		
<i>S. columbaria</i>	l.	l.	<i>Barbula fallax</i>	o.	—
<i>S. succisa</i>	l.	l.a.	<i>Brachythecium purum</i>	a.	a.
<i>Senecio erucifolius</i>	—	l.	<i>Camptothecium lutescens*</i>	a.	a.
<i>S. jacobaea</i>	—	r.	<i>Fissidens taxifolius</i>	—	o.
<i>Thymus serpyllum</i>	a.	a.—l.d.	<i>Hylocomium triquetrum</i>	l.a.	l.a.
<i>Trifolium pratense</i>	o.	l.	<i>Hypnum cupressiforme</i>	—	l
<i>T. procumbens</i>	o.	o.	<i>var. elatum</i>		
<i>T. repens</i>	l.	o.	<i>H. molluscum*</i>	f.	l.a.
<i>Trisetum flavescens</i>	a.	o.	<i>Neckera crispa*</i>	—	a.
<i>Tussilago farfara</i>	r.	r.		Total 5	7
<i>Ulmaria palustris</i>	—	r.			
<i>Verbascum nigrum</i>	r.	r.		85	107

## D. DOWNLEY GRASSLAND.

The area of chalk grassland which we have studied most closely is that occupying the slopes above Downley Bottom (8 and 9) on the Ditcham Park estate. This area is on the extreme east of the region dealt with in this paper, and just within the county of Sussex. Natural chalk woodland, consisting mainly of beech, ash, yew, and whitebeam (beech-associates of Dr A. S. Watt<sup>1</sup>), covers the upper part of the slope, which is continuous with the plateau of West Harting Down, covered with a very flinty non-calcareous soil. In addition to the above mentioned trees the plateau wood contains a good deal of *Quercus robur* and some *Betula alba* (ash-oak associates of Watt<sup>1</sup>). The lower slopes and the Bottom itself are covered with chalk grassland on which sheep had long been pastured.

<sup>1</sup> Watt. This JOURNAL, 12, p. 176.



Phot. 1. Downley Bottom, A area. Sept. 1911. The tall isolated plants are *Cirsium palustre*.



Phot. 2. Downley Bottom, B area. Sept. 1912. The outer fence has been recently added. The hummocky turf is due to the action of moles. *Cirsium palustre* is here seen inside the enclosure only.



In 1908 the whole area was heavily infested with rabbits, whose burrows were very numerous, so that the herbage of the pasture averaged half an inch (1.25 cm.) to one inch (2.5 cm.) in height, and the shrubs and trees on the edge of the wood were eaten back and quite prevented from advancing. During the winter of 1908-9 two areas of approximately 820 sq. metres (980 sq. yards) and 390 sq. metres (470 sq. yards) respectively were enclosed with rabbit proof fencing, the upper fence in each case running within the fringe of shrubs on the edge of the wood. The primary object of these enclosures was to determine whether the grassland would be colonised by shrubs and trees when browsing and nibbling animals were excluded. The results of the observations on this point have been published in No. 2 of these 'Studies'<sup>1</sup>. The withdrawal of rabbit attack of course affected the grassland itself, and the changes occurring, noted superficially up to 1913, were more carefully studied in 1914 and again in 1920.

The two areas at the time of enclosure were perfectly typical examples of the surrounding vegetation. The larger area "A" (8) has a north-western exposure and a uniform inclination of 17° or 18°. It also has a somewhat different surface soil (see below) from the smaller "B" (9) which has a western exposure, and an inclination varying from 15° to 23°. These differences are reflected in the vegetation.

The following are transcripts from the brief field notes of the earlier years:

*July, 1909. Area A.* Turf closed, closely nibbled ( $\frac{1}{2}$ "-1") outside, herbage averaging 5 inches (12.5 cm.) and much greener inside enclosure. Few flowers outside (*Lotus corniculatus*, *Prunella vulgaris* and a little *Thymus serpyllum*). Inside *Lotus* and *Prunella* flowering more freely<sup>2</sup>.

*Composition of turf.* A basis of moss, mainly *Brachythecium purum* and *Hylocomia*, formed the lower stratum where the turf was deep enough. Where the turf was most closely nibbled the mosses were codominant with the grasses and dicotyledonous herbs, or even dominant, especially close to the edge of the wood where they were most shaded. No one species was dominant in the upper stratum of turf. The following species of flowering plants were noted, the first eight being especially conspicuous, in the order in which they are given:

<i>Festuca ovina</i>	<i>Plantago lanceolata</i>	<i>Cirsium lanceolatum</i>
<i>Carex flacca</i>	<i>Polygala vulgaris</i>	<i>C. palustre</i>
<i>Asperula cynanchica</i>	<i>Thymus serpyllum</i>	<i>Hieracium pilosella</i>
<i>Poterium sanguisorba</i>	<i>Leontodon hispidus</i>	<i>Fragaria vesca</i>
<i>Lotus corniculatus</i>	<i>Achillea millefolium</i>	<i>Viola silvatica</i> (agg.)
<i>Prunella vulgaris</i>	<i>Myosotis arvensis</i> (outside)	<i>Linum catharticum</i>
<i>Avena pratensis</i>	<i>Euphrasia nemorosa</i>	<i>Origanum vulgare</i>
<i>Agrostis tenuis</i>	<i>Trifolium pratense</i>	<i>Veronica officinalis</i>
	<i>Ranunculus bulbosus</i>	<i>Galium erectum</i>
<i>Viola hirta</i>	<i>Cirsium acaule</i>	<i>Alchemilla arvensis</i>
<i>Galium verum</i>		

[No separate lists were made of species occurring inside and outside the fenced area, but it is unlikely that any difference in specific composition would arise during a single growing season. A conspicuous feature was 16 tall flowering plants of *Cirsium palustre* within the enclosure, there being none on the rabbit-nibbled turf outside.]

<sup>1</sup> Tansley. This JOURNAL, 10, pp. 168-177.

<sup>2</sup> Cf. Farrow. This JOURNAL, 5, pp. 3, 4.



*Area B.* Turf of the same general type as A, but herbage thicker, less moss, much less *Carex flacca*. Also much *Helianthemum vulgare*, and *Potentilla erecta* (not seen in A). There were about 65 tall flowering specimens of *Cirsium palustre* within a space of about 600 square feet within the enclosure. (Three of the thistles can be seen in Plate III, Fig. 2; this photograph was taken in 1912.)

In September, 1911, at the end of a very hot dry summer, two American ecologists who visited the areas remarked that the vegetation inside the enclosures reminded them of, and strongly resembled in general character, that of the *drier* prairies of the "middle west." (Cf. photograph of the corner of A enclosure, Plate III, Fig. 1.)

In 1913 more exhaustive lists were made of the species growing inside and outside the two enclosures, while in 1914 and again in 1920 the vegetation was thoroughly studied.

*Height of the herbage.* During the years from 1908 to 1914 measures had been taken to diminish the number of rabbits on the Downley area at large, and the effect of this was now seen.

In 1920 the rabbit pressure had evidently still further diminished, and cattle instead of sheep were now pastured. The following table gives the general height of the herbage in centimetres at the three periods.

Table V. *Height of herbage at Downley (cm.).*

	Unenclosed		Enclosed	
	A	B	A	B
1909	1-2.5	1-2.5	12.5	14
1914	2.5-5	4-8	10-15	15-22.5
1920	4-8	4-9	15-30	20-25

*Changes in the herbaceous vegetation. Area B, August, 1914.* A much greater mass of grass herbage within the enclosure as opposed to *Poterium*, *Helianthemum* and *Lotus* without. These three form the conspicuous plants outside, with blades of *Festuca ovina* and *Carex flacca* protruding between. This is no doubt an effect of differential nibbling, the rabbits preferring the grass to anything else. *Cirsium acaule* and *C. palustre* are also much more conspicuous without than within (Pl. IV, Fig. 3), their basal rosettes often suppressing the surrounding plants<sup>1</sup>. But though altering the proportions and relative conspicuousness of different plants, the rabbits do not appear to have made much difference within the six years to the list of herbaceous species. The decrease in the number of rabbits has simply enabled the grasses to shoot up more freely through the other plants.

Inside the enclosure some species have suffered more or less seriously from the effects of competition: *Helianthemum*, which covers the mole heaps outside is not holding its own inside, while *Lotus* and *Poterium* are scarcely so conspicuous as they were. The last-named however holds its own pretty well with the grasses, developing larger leaves and *alternating* with the grasses

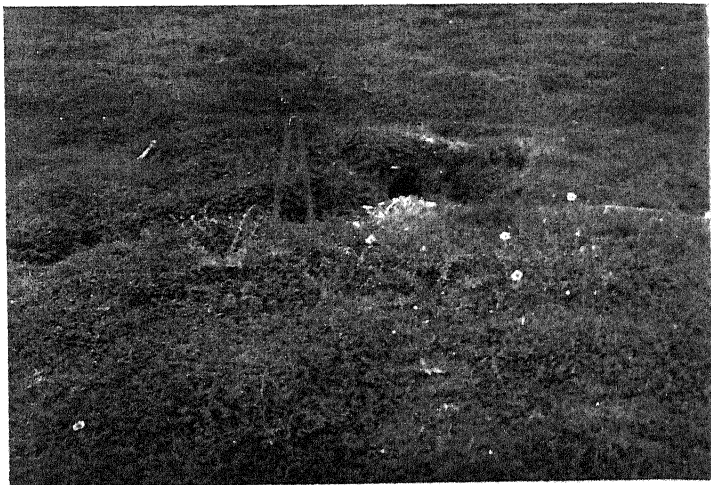
<sup>1</sup> Cf. Lindman. "Some cases of plants suppressed by other plants." *New Phytologist*, 12, 1913, p. 1.



Phot. 1. Inside enclosure. Clans of *Holcus lanatus* (left and centre) and *Galium verum* (centre and right). *Poterium sanguisorba* and *Agrostis tenuis* are also visible. Herbage at least 8 inches deep. Sept. 1914.



Phot. 2. Inside enclosure. *Calluna vulgaris* (fl.) centre, *Potentilla erecta* (fl.) right centre. *Galium verum* and *Avena pratensis* (front) are also seen. Herbage about 6 inches deep. Sept. 1914.



Phot. 3. Outside enclosure. Hummocky ground with rabbit hole and short turf. *Helianthus*



in clumps or areas more than it does outside. The thistles are no longer able to keep their basal rosettes spread out, and *Cirsium acaule* develops stalks to its heads. *Galium verum* holds its own particularly well with the grasses and forms a fair proportion of the herbage (Pl. IV, Fig. 1, right). *Thymus*, on the other hand, is almost entirely suppressed, and *Potentilla erecta* often suffers and is unable to flower, though it produces long thin stems. The mosses, also, are so much shaded that they are often etiolated.

*September, 1920.* Mole heaps very numerous outside the enclosure and comparatively few within. This affects the general physiognomy of the vegetation because *Thymus* and *Helianthemum* dominate the mole heaps. The preponderance of grass inside the enclosure is marked, but *Poterium sanguisorba* is now quite holding its own owing to its local dominance. It is freely attacked by *Phragmidium sanguisorbae* as in 1914, but this has not affected its success. Outside the enclosure there is more *Lotus* and *Potentilla* in proportion to *Achillea millefolium* and *Galium verum* than inside. The thistles are not quite so strong outside as they were in 1914. Some rosettes are being pressed back and others overgrown by the more luxuriant growth of the other herbage consequent on the decreased rabbit pressure. Inside they are suffering severely, there being no seedlings of *C. palustre*. In 20 quadrats, each of a quarter of a square metre, taken at random from inside the enclosure (= 5 sq. m. in all) there were 10 plants of *C. palustre*, as compared with 21 outside in 20 equal quadrats. In the same area there were 31 plants of *C. acaule* inside as compared with 79 outside.

In order to obtain a measure of the difference in the bulk of the various species developed the herbage was cut from an area of .25 sq. m. inside and another of the same size outside the enclosure, the plants being cut off with a razor as close as possible to the surface of the soil. Each lot of herbage was weighed fresh and was then thoroughly mixed and a sample of about a quarter taken. This sample was sorted into nine fractions, the most prominent species being weighed separately. The results are given below.

Table VI. *Weights of herbage at Downley.*

Total fresh weight of herbage from .25 m. <sup>2</sup> outside enclosure = 163.5 gm.				
" " " " inside " = 283.2 gm.				
Outside			Inside	
	Grams	Per cent. of total	Grams	Per cent. of total
Grasses	19.6	41.6	52.0	67.2
<i>Poterium sanguisorba</i>	4.6	9.7	17.1	22.1
<i>Helianthemum vulgare</i>	5.6	11.9	0.9	1.1
<i>Lotus corniculatus</i>	3.8	8.0	0.1	0.13
<i>Cirsium acaule</i>	6.8	14.4	Nil	Nil
<i>Plantago lanceolata</i>	0.9	1.9	0.25	0.33
<i>Galium verum</i>	Nil	Nil	2.2	3.4
Mosses	0.5	1.0	0.65	0.84
Residue	5.4	11.4	3.2	4.8
Total samples sorted and separately weighed	47.2	100.0	76.4	100.0

These figures, while they do not of course give an accurate measure of the actual proportions of the various species in the whole enclosed area compared with the unenclosed grassland outside, nevertheless bring out some interesting points. First, the weight of herbage inside the enclosure is not quite doubled, though its height is increased from three to five times. This is owing to the much greater "solidity" of the vegetation in the short rabbit-nibbled turf carpet. Secondly, the grasses form well under half the weight of the herbage outside, while inside they make up more than two-thirds and *Poterium* nearly one-quarter. Thirdly, there is greater approach to equality in the proportions of several different species in the short turf outside, and a greater dominance of a few among the taller vegetation inside the enclosure. Only the grasses and *Poterium* exceed 5 per cent. of the total weight inside the enclosure, while the grasses and four other species of those weighed each forms 8 per cent. or more outside, and the "residue" of species not separately weighed amounts to 11.4 per cent. outside and only 4.8 per cent. inside.

Table VII. *Species flowering in September 1920 on Area B at Downley.*

	Outside	Inside		Outside	Inside
<i>Achillea millefolium</i>	.	x	<i>Hypericum perforatum</i>	Absent	x
<i>Calluna vulgaris</i>	Absent	x	<i>Leontodon autumnalis</i>	x	x
<i>Campanula rotundifolia</i>	x	x	<i>L. hispidus</i>	x	x
<i>Clinopodium vulgare</i>	Absent	x	<i>Linum catharticum</i>	x	.
<i>Cirsium acaule</i>	x	x	<i>Lotus corniculatus</i>	x	x
<i>C. palustre</i>	x	x	<i>Plantago lanceolata</i>	.	x
<i>Euphrasia nemorosa</i>	x	Absent	<i>P. media</i>	.	x
<i>Galium erectum</i>	Absent	x	<i>Potentilla erecta</i>	x	x
<i>G. mollugo</i>	"	x	<i>Prunella vulgaris</i>	x	x
<i>G. verum</i>	x	x	<i>Senecio jacobaea</i>	x	x
<i>Helianthemum vulgare</i>	x	x	<i>Scabiosa columbaria</i>	x	x
<i>Hieracium pilosella</i>	x	Absent	<i>Trifolium pratense</i>	x	.
			Total	16	20

Of these species 12 were flowering both inside and outside the enclosure. Of the four flowering outside and not inside two are apparently now absent inside owing to competition, and the other two have decreased decidedly in abundance. Of the eight flowering inside and not outside, five are absent outside, and the other three have tall conspicuous inflorescences specially likely to be eaten off.

In the early years of enclosure, when the rabbit pressure was more severe outside, the discrepancy in the numbers of species flowering inside and outside the enclosure was undoubtedly much greater, for then the number of species flowering outside was very small indeed, while the number flowering inside was at a maximum. The present tendency is to a decrease in the number flowering inside owing to the increasing dominance of a few species and the suppression of others, while the diminution of rabbit pressure has substantially increased the number that can flower outside.

#### *Soils of the Downley Areas.*

The surface soil of the A area is a dark brown humous loam, very rich in carbonates, about 4 inches (10 cm.) deep and densely matted with the roots

and rhizomes of the close herbage. The next four inches, i.e. down to a depth of 20 cm. from the surface, contain many fewer roots, much less humus and a gradually increasing number of small chalk lumps. At about this level the chalk rock is *in situ* but the upper surface is much fissured, with brown loam occupying the cracks. In this the roots of the deeper rooting species pass down to a depth of at least 30 cm. from the surface.

Table IX. *Soils of the Downley areas. Chemical analyses, September, 1920.*

Area	Depth inches	Sample	Water lost in air drying	Water lost at 100° C.	Loss on ignition	Total carbonates	Nitrates as NaNO <sub>3</sub>	P <sub>2</sub> O <sub>5</sub>	K <sub>2</sub> O	MgO	CaO	Insol. residue	pH (Wherry's indicators)	Specific acidity
A. Outside	0-4	D 6	39.8	8.0	21.36	36.0	.0036	.166	.267	.061	18.27	27.5	7.5	-3
"	4-8	D 7	33.0	9.6	5.48	62.1	.0060	.161	.374	.221	36.13	16.5	—	—
" Inside	0-4	D 4	37.8	8.4	23.20	26.1	.0080	.269	.510	.350	18.79	27.0	7.5	-3
"	4-8	D 5	30.6	4.0	16.32	72.0	.0025	.151	.211	.073	35.05	9.0	—	—
B. Outside	0-1	D 3	26.8	6.2	24.0	2.4	.0036	.149	.341	.198	1.11	54.5	} 7	1 (neutral)
"	1-5	D 13	28.0	6.0	14.11	5.33	.0119	.058	.408	.201	3.50	77.2		
"	5-8	D 14	23.6	4.0	4.6	19.3	.0045	.156	.407	.037	10.21	45.5		
" Inside	0-1	D 2	31.8	7.5	39.20	2.8	.0119	.188	.384	.099	1.69	51.3	} 6.5	+3
"	1-5	D 11	28.0	6.9	16.14	5.6	.0040	.157	.340	.231	3.26	59.1		
"	5-8	D 12	24.8	5.2	14.19	10.6	.0033	.174	.421	.001	5.31	58.5		

Inside the enclosure the surface humous soil is distinctly deeper, the loss on ignition of the first 8 inches (20 cm.) being 19.76 per cent. against 13.42 per cent. outside. The reaction in both cases is distinctly alkaline (pH 7.5, specific alkalinity 3). Chalk *in situ* is met with at 25 cm. and solid unfissured chalk at 38-40 cm. from the surface. Thus the enclosure for eleven years has resulted in a marked increase in the accumulation of surface humus, giving an increased depth of about 5 cm.

The soil of the B area is a somewhat lighter brown, more powdery loam. The whole 8 inches (20 cm.) taken from outside the enclosure shows almost the same loss on ignition (14.08 per cent.) as the corresponding sample from A (13.42), but only one-fifth the percentage of carbonates (10.2 against 49.05). The top inch is absolutely poor in carbonates (2.4 per cent.) and the next 4 inches (5.33) poor for a chalk soil; there is a correspondingly high percentage of insoluble material. The reaction of the top 4 inches is neutral. The chalk *in situ* occurs at a depth comparable with that obtaining in the A area.

Inside the enclosure, while the lime figures of the top 5 inches are very similar to those outside, the accumulation of humus in the top inch is very marked (39.20 per cent. loss on ignition). The percentage of carbonates for the whole 8 inches is only 7.1, against 10.5 outside and 49 for the corresponding depth of soil in A, and the reaction of the upper layers is distinctly acid.

Two points of difference between the areas are clear. First, the soil of the B area overlying the chalk rock is much poorer in lime and richer in insoluble constituents. Secondly, the accumulation of humus in the top layers within the enclosure is much greater in B than in A, and the reaction is more acid. Nitrates, phosphates and potash all appear to have accumulated in the top layers inside the enclosures. The vegetation and its changes during the period of enclosure reflect these differences.

Table VIII. Floristic composition of the herbage of Areas A and B at Downley.

<p>The table below gives a complete list of the species occurring on the two areas in 1914 and 1920, with frequency symbols and notes. Lists made in 1913 are also incorporated, but the frequency symbols are incomplete. A × signifies presence where a frequency estimation was not made. A ? signifies probable undetected presence. An asterisk indicates a member of the wood-edge community, a dagger species belonging to the dry chalk bank casual community. Square brackets include the names of casual species, not belonging to any of these communities, which have colonised patches of bare soil.</p>																			
	General Downley grass land	Area A										Area B						Notes	
		Outside enclosure					Inside enclosure					Outside enclosure			Inside enclosure				
		1913	1914	1920	1913	1914	1913	1914	1920	1913	1914	1914	1920	1914	1920	1914	1920		
<i>Aceras anthropophora</i>	r.	—	r.	—	—	—	—	r.	—	—	—	—	f.	—	—	—	—	Increasing inside enclosures	
<i>Achillea millefolium</i>	f.	f.	a.	f.—l.a.	a.	a.	a.	a.	a.l.d.	—	—	—	f.	f.	f.	v.a.	v.a.		
<i>Agrostis tenuis</i>	f.—a.	—	f.	f.—l.a.	o.—a.	—	—	—	l.	—	—	—	a.	a.	a.	v.a.	f.	Decreasing inside enclosures owing to competition	
<i>A. alba</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>Anthoxanthum odoratum</i>	o.	—	—	—	—	—	—	—	—	—	—	—	—	—	o.	l.v.a.	l.a.	Decreasing owing to competition in enclosures	
<i>Asperula cynanchica</i>	a.	—	—	f.	—	×	a.	o.	—	—	—	—	a.	o.	f.	—	—		
* <i>Atropa belladonna</i>	l.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	New colonist	
<i>Avena pratensis</i>	a.	—	f.	f.	×	c.o.d.	v.a.	—	—	—	—	f.	f.—l.a.	f.	l.v.a.	f.—a.	—		
<i>A. pubescens</i>	a.	—	—	—	—	—	—	—	—	—	—	—	f.	f.	l.	o.	—	Very likely missed in outside turf: apparently decreasing inside owing to competition	
<i>Bellis perennis</i>	f.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>Brachypodium silvaticum</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	Invading	
<i>Briza media</i>	o.	—	o.	—	×	f.	o.	—	—	—	—	—	—	—	f.	o.	—		
<i>Bromus erectus</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	l.	Colonised enclosure about 1911, increasing	
<i>Bryonia dioica</i>	r.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	l.	l.		
<i>Calluna vulgaris</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	Practically constant but rather more outside	
<i>Campanula glomerata</i>	r.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>C. rotundifolia</i>	a.	o.	f.	a.	×	—	o.	f.	f.	—	—	o.	o.—f.	o.	o.	a.	a.	Increases at first with lessening rabbit pressure, then begins to give way to competition of grasses	
<i>Carex flacca (glauca)</i>	v.a.	a.	l.s.d.	va—l.d.	a.	co.d.	v.a.	—	—	—	—	v.a.	v.a.	a.	a.	a.	a.		

C. praecox (caryophyllea)						x	?	a.	f.	L.a.	r.	—	Apparently disappeared in B enclosure
Carlina vulgaris													? Invading
Centaurea nigra									r.				Mole heaps
Cerastium vulgatum										a.		r.	Certainly decreased owing to competition in enclosures
Cirsium acule	a.	f.	a.	f.			f.			f.	a.	o.	Bare places]
[C. arvense	i.	a.					l					—	Decreasing in B enclosure
[C. lanceolatum			r.				a.				r.	o.	Local on wood edge, increasing in B enclosure
[C. palustre	f.	a.	f.	f.			l.			f.	l.	l.	On bare soil]
*Clinopodium vulgare			l.	x			l.						
[Cynoglossum officinale	l.		l.r.										
Cynosurus cristatus	r.												
Daucus carota													
Dactylis glomerata													Invasive
Euphrasia brevipila													Decreasing owing to competition
Euphrasia nemorosa	f.—la.	x	f.	f.			o.	v.a.	d.	a.	l.d.		Decreasing inside enclosures owing to competition of other grasses, still dominant on mole-heaps
Festuca ovina	v.a.—c.d.	c.d.	d.	e.d.	a, l.d.	d.	v.a.						Increasing in enclosures
F. rubra	—												Increasing inside enclosures in single patches
*Fragaria vesca	l.	r.	l.a.	x			o.	y.a.					Invading
Galium erectum	o.		r.					l.					
*G. mollugo	—												
G. verum	a.	f.	o.—f	f.	a.	o.	o.	f.l.a.	v.a.	a.	l.d.	v.a.	
Gentiana amarella	o.	f.	o.—r.	o.—r.									Decreasing
Hellanthemum vulgare	la.—l.d.												Especially dominant on mole-hills
+Hieracium pilosella	la.		l.	l.			l.	x	l.a.	f.			On bare soil, decreasing with the decrease of this
Hippocrepis comosa													
Holcus lanatus	o.												Increasing in B enclosure
*Hypericum hirsutum													Invading from wood edge
Hypochoeris radicata													Increasing slightly from wood edge
Koeleria gracilis	o.												
Leontodon autumnalis	f.—la.	o.	f.	x									
L. hispidus	f.	a.	o.—f.	a.									Not often flowering outside
Leucanthemum vulgare													
Linum catharticum	f.	f.	f.	o.			r.	l.	o.	f.	x	r.	



Table VIII (continued).

	Area A						Area B				Notes
	Outside enclosure			Inside enclosure			Outside enclosure		Inside enclosure		
	1913	1914	1920	1913	1914	1920	1914	1920	1914	1920	
General	1914										
Lotus corniculatus	v.a.										Increasing outside, decreasing inside
Luzula campestris	—										On freshly turned soil
Myosotis arvensis	—										Round holes dug in 1919]
+Organum vulgare	—										
[Pastinaca sativa]	—										
Pimpinella saxifraga	—										
Pimpinella saxifraga	f.	a.	var.l.d.	×	a.	l.	l.f.	f.	f.—a.	f.—l.a.	
Plantago lanceolata	o.	—	—	×	—	—	o.—f.	r.	o.	r.	
P. media	—	—	—	—	—	—	—	—	—	—	
Poa pratensis	—	—	—	—	—	—	—	—	—	—	
Polygala vulgaris	o.	—	—	—	—	—	—	—	—	—	
Potentilla anserina	l.a.	—	—	—	—	—	—	—	—	—	
P. erecta	o.—f.	—	—	—	—	—	o.—f.	—	—	—	
*P. sterilis	—	—	—	—	—	—	—	—	—	—	
Poterium sanguisorba	v.a.	l.a.	l.a.	a.	l.a.	a.l.d.	a.l.d.	a.l.d.	f.—v.a.	a.l.d.	A wood edge plant, beginning to invade
Primula veris	—	—	—	×	—	4	×	l.	×	r.	Local dominance increasing in enclosures
Prunella vulgaris	a.	f.	o.—f.	f.	f.	—	o.	o.	o.	o.	Small patches increasing in number
Ranunculus bulbosus	o.	—	—	—	—	—	—	—	—	—	
R. repens	—	—	—	—	—	—	—	—	—	—	
Rumex acetosa	—	—	—	×	—	—	—	—	—	—	Increasing both inside and outside
Scabiosa columbaria	r.	—	o.	×	—	—	×	o.	r.	l.	One patch has established itself in A encl.
S. succisa	—	—	r.	×	—	—	—	—	—	—	By new fence]
Senecio crucifolius	f.	×	o.	—	—	—	—	—	—	—	
S. jacobaea	—	—	—	—	—	—	—	—	—	—	
[Sonchus asper	o.	—	—	—	—	—	—	—	—	—	Decreasing in enclosures generally: local occurrence is on mole heaps
Taraxacum officinale	r.	—	—	—	—	—	—	—	—	—	
Tenurem scorodonia	a.	f.	l.a.	f.	o.	l.	—	l.a.	o.	l.	
Thymus serpyllum	—	—	—	—	—	—	—	—	—	—	

<i>Trifolium pratense</i>	f.	x	f.	o.	—	r.	f.	f.	r.	o.	r.	Decreased on the whole
<i>T. repens</i>	o.	—	f.	o.—r.	—	—	—	—	—	—	—	"
<i>Trisetum flavescens</i>	—	—	—	—	—	l.	—	—	—	r.	—	Probably missed outside
[ <i>Urtica dioica</i>	—	—	—	—	—	—	—	—	—	—	—	
[ <i>Veronica arvensis</i>	r.	—	—	—	—	la.	—	—	—	o.	r.	On freshly turned soil]
* <i>V. chamaedrys</i>	o.	—	l.	o.	x	l.	—	la.	—	—	l.	Apparently decreasing in enclosures
<i>V. officinalis</i>	o.	—	r.	o.	—	—	—	—	—	—	l.r.	
<i>Viola riviniana</i>	—	—	—	f.	—	o.	—	—	—	o.	—	
* <i>V. silvestris</i>	la.	o.	f.	f.	x	a.	—	la.	—	f.	—	
<i>V. hirta</i>	f.—la.	la.	a.	a.	a.	—	—	—	—	—	—	
+ <i>Verbascum nigrum</i>	r.	—	—	—	—	—	—	—	—	—	—	
+ <i>V. thapsus</i>	r.	—	—	—	—	—	—	—	—	—	—	
<i>Barbula unguiculata</i>	—	—	—	—	—	—	—	—	—	—	l.	On bare soil
<i>Brachythecium glareosum</i>	—	—	—	—	—	—	—	?	—	?	o.	Probably not distinguished in 1914 from <i>B. parvum</i>
<i>B. purum</i>	v.a.	co—d.	f.	f.	x	f.	a.l.d.	a.	—	a.	r.	Especially under grasses, dominance decreasing
<i>Bryum capillare</i>	l.	—	—	—	—	—	—	—	—	—	r.	Bare soil
<i>Campothecium lutescens</i>	a.	—	—	l.	—	—	o.	a.	—	o.	o.	Especially rabbit burrows and mole heaps
<i>Dicranum scoparium</i>	o.	x	a.	la.	l.	f.	o.	o.	—	—	—	
<i>Fissidens taxifolius</i>	o.	—	—	—	—	—	—	—	—	—	—	
<i>Eurhynchium praelongum</i>	—	—	—	—	—	—	—	—	—	—	o.	
<i>E. swartzii</i>	la.	a.	a.	f.	x	a.	f.l.a.	—	—	o.—f.	—	
<i>Hylacomium splendens</i>	—	—	—	—	—	—	—	—	—	—	—	Decreases with decreased rabbit pressure, i.e. with increased growth of herbs
<i>H. squarrosum</i>	la.	co—d.	l.s.d.	co—d.	x	l.s.d.	l.s.d.	o.	x	f.	Below herbage inside enclosures, increasingly etiolated	
<i>H. triquetrum</i>	la.	x	s.d.	f—a.	x	a.	a.l.d.	a.	x	a.	Especially under grass, increasing inside both enclosures	
<i>Hypnum cupressiforme var.</i>	o.	a.	x	la.	?	o.	l.	r.	—	—	? Decreasing	
<i>H. elatum</i>	—	?	?	o.	?	f.	o.	—	—	o.	o.	
<i>H. cuspidatum</i>	—	—	—	—	—	—	—	—	—	—	—	
<i>Mnium affine</i>	—	—	—	—	—	—	—	—	—	—	—	
<i>Neckera crispa</i>	f.	—	—	—	—	—	—	l.	—	—	—	
<i>Pottia lanceolata</i>	—	—	—	—	—	—	—	—	—	—	r.	Bare soil
<i>Cladonia fimbriata</i>	o.l.	—	—	—	—	—	—	o.	—	—	—	
<i>C. silvatica</i>	o.l.	—	—	—	—	—	—	l.	—	—	—	

Figs. 3 to 6 illustrate four quadrats, each 2.5 dm. (about 10 inches) square outside and inside the enclosure B in 1914 and 1920. The areas charted are unfortunately not the same, because the wooden marking pegs disappeared during the six-year interval, but 3 is very close to 5 and 4 to 6, while all four represent turf which was originally (in 1908) closely similar. The striking points are the very great diminution of the number of individual plants (cf. Figs. 3 and 4) other than *Festuca ovina* (which increased enormously) as a result of the first six years' enclosure and withdrawal of all grazing and nibbling, and the smaller though still marked diminution (cf. Figs. 3 and 5) as the result of the lessened nibbling outside the enclosure during the second six years. During this second period too the other plants increased in number (cf. Figs. 4 and 6) inside the enclosure at the expense of *Festuca ovina* which decreased markedly and lost dominance (Figs. 7 and 8).

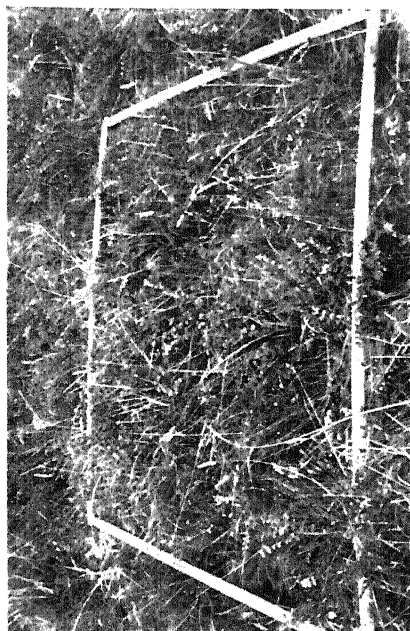
Compare also Plate V, Figs. 1, 2 and 4.

#### DESCRIPTION OF FIGURES 3-6.

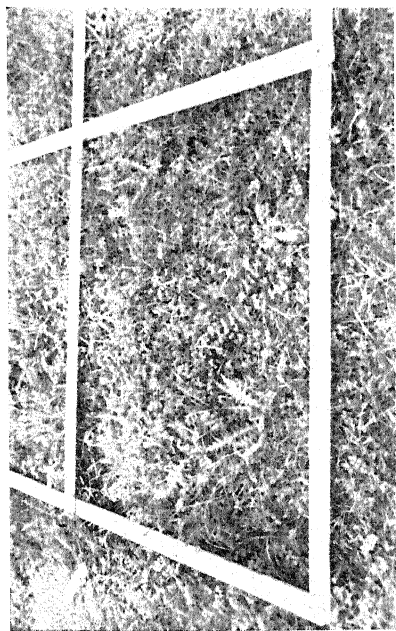
- FIG. 3. Quadrat 2.5 dm. square (=6.25 square dm.) outside the Downley "B" enclosure in August, 1914. Herbage 4-5 cm. high. *Festuca ovina* (not represented on the chart) was dominant, filling all spaces between the other plants. The flat rosettes of *Cirsium acaule* and *C. palustre*, whose leaves are diagrammatically represented, were conspicuous, and occupied a considerable area. The total number of rooted shoots of flowering plants, other than *Festuca ovina*, is approximately 431.
- FIG. 4. Quadrat of same size inside the Downley "B" enclosure, Sept. 1914. Herbage about 18-20 cm. high (mosses not recorded). *Festuca ovina* (not represented on the chart) was dominant, filling all spaces on the surface of the turf between the other plants, though there were bare spaces on the soil surface, concealed by the mass of vegetation. The total number of other flowering plants was only 20 (in some other quadrats of the same size as many as 40 occurred), but the individual plants were much bigger, as is roughly indicated by the size of the letters used as symbols. The effect of the complete withdrawal of grazing and nibbling was primarily to allow the growth of the dominant grass to the suppression of the great majority of the other flowering plants.
- FIG. 5. Quadrat of same size outside the enclosure, Sept. 1920. During the six years from 1914 to 1920 the rabbits in the area had been considerably reduced, cattle instead of sheep were grazed and the depth of the herbage had increased to a height of 6-7 cm. *Festuca ovina* was still dominant, filling all spaces, and the less severe grazing and nibbling had again encouraged its growth, at the expense of the other flowering plants which now numbered about 233. Many of the latter had produced semi-procumbent shoots (indicated by arrows).
- FIG. 6. Quadrat of same size inside the "B" enclosure, Sept. 1920. Herbage 20-25 cm. high. In spite of the increased height of the herbage it was less dense, and many bare spaces existed on the soil though none on the surface of the herbage. *Festuca ovina* was still very abundant (see Fig. 7), but no longer filled all the gaps between the other plants, which numbered 52 individuals (in other quadrats of the same size more than 80 existed), the other species profiting at the expense of the sheep's fescue.



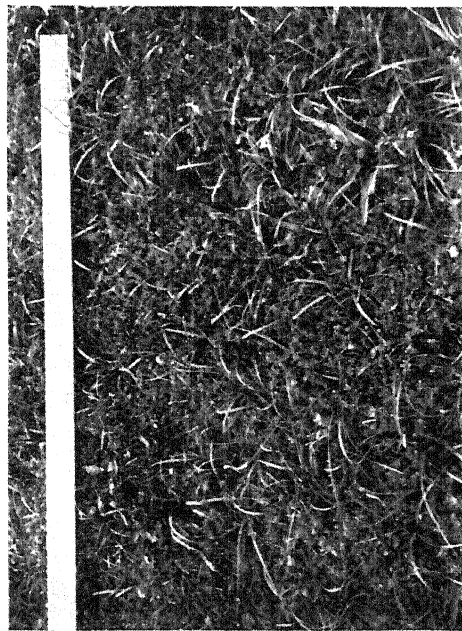
Phot. 2. Outside enclosure B. Quadrat 5 dm. square. *Festuca ovina*, *Poterium sanguisorba*, *Carex flacca*, *Cirsium polsterii*, *Viola hirta*, etc. Sept. 1920.



Phot. 4. Inside B enclosure. Metre quadrat. Fig. 8 is the lower half of this. Deep herbage (8 to ins.) of *Poterium sanguisorba*, *Arvensis*, *Helianthemum*, *Holcus lanatus*, etc.



Phot. 1. Outside enclosure B. Quadrat 5 dm. square. *Festuca ovina*, *Poterium sanguisorba*, *Cirsium acule*, *Carex flacca*, etc. Sept. 1914.



Phot. 3. Area A outside enclosure, close to edge of wood. *Hylaeonium squarrosum*, *H. splendens*, *Carex flacca*, *Cirsium squarrosum*, etc. The photograph shows carex rather more than in 1914.



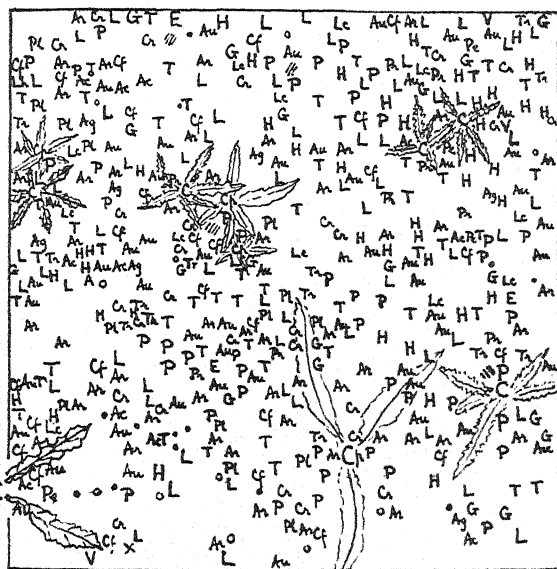


FIG. 3. Outside, 1914.

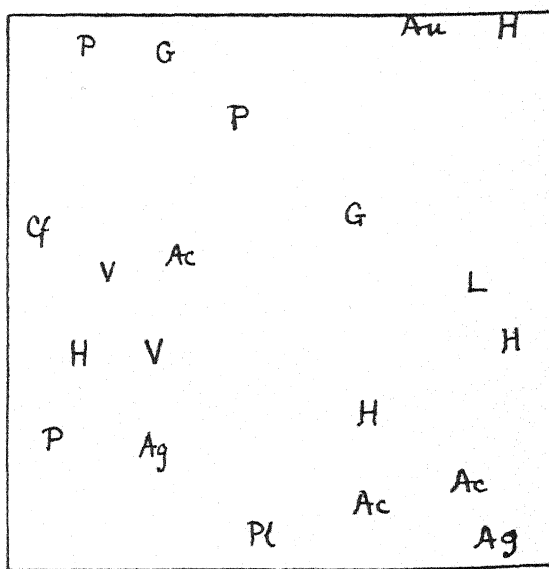


FIG. 4. Inside, 1914.

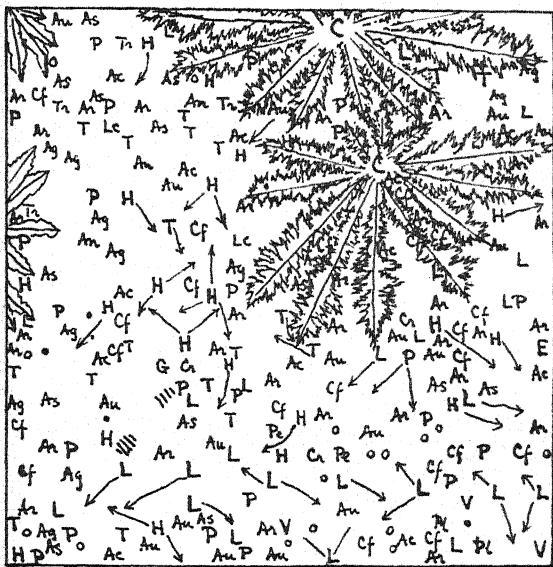


FIG. 5. Outside, 1920.

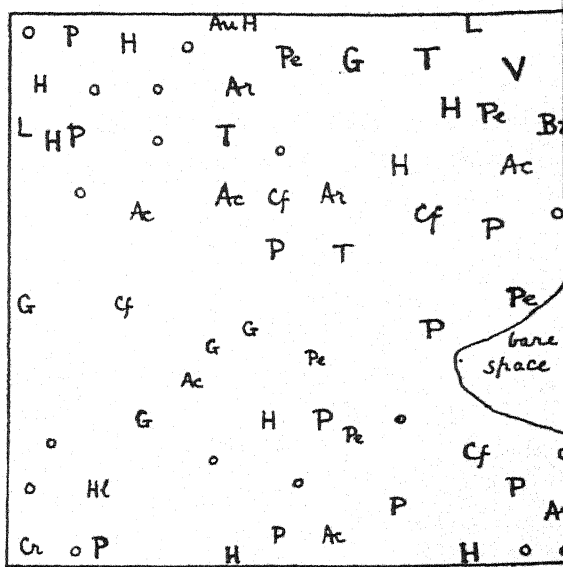


FIG. 6. Inside, 1920.

List of plants, with symbols and numbers of individuals occurring in the quadrats represented in Figs 3, 4, 5, 6 and 8.

		Fig. 3		Fig. 4		Fig. 5		Figs. 6 and 8	
		No.	%	No.	%	No.	%	No.	%
<i>Achillea millefolium</i>	Ac	8	2	3	15	12	6	73	10.0
<i>Anthoxanthum odoratum</i>	An	—	—	—	—	3	1.5	9	1.3
<i>Agrostis tenuis</i>	Ag	6	1.5	2	10	11	5	6	0.8
<i>Asperula cynanchica</i>	As	—	—	—	—	13	6	10	1.5
<i>Avena pratensis</i>	Ar	53	12	—	—	31	15	52	7.0
<i>A. pubescens</i>	Au	52	12	1	5	17	8	15	2.0
<i>Brachypodium silvaticum</i>	Bs	—	—	—	—	—	—	1	0.1
<i>Briza media</i>	Bz	—	—	—	—	—	—	3	0.4
<i>Bromus erectus</i>	Be	—	—	—	—	—	—	1	0.1
<i>Campanula rotundifolia</i>	Cr	27	6	—	—	3	1.5	14	2.0
<i>Carex flacca (glauc)</i>	Cf	25	6	1	5	20	10	48	7.0
<i>Cirsium acaule</i>	C	6	1.5	—	—	2	1	—	—
<i>C. palustre</i>	Cp	4	0.9	—	—	—	—	2	0.3
<i>Cynosurus cristatus</i>	Cy	—	—	—	—	—	—	1	0.1
<i>Euphrasia nemorosa</i>	E	2	0.5	—	—	1	0.5	—	—
<i>Galium erectum</i>	Ge	—	—	—	—	—	—	5	0.7
<i>G. verum</i>	G	19	4.3	2	10	1	0.5	71	10.0
<i>Helianthemum vulgare</i>	H	41	9	4	20	21	10	101	14.0
<i>Holcus lanatus</i>	Hl	—	—	—	—	—	—	56	8.0
<i>Leontodon hispidus</i>	Lh	1	0.2	—	—	—	—	—	—
<i>Linum catharticum</i>	Lc	11	2.6	—	—	2	—	—	—
<i>Lotus corniculatus</i>	L	62	14	1	5	25	12	44	6.0
<i>Luzula campestris</i>	Lz	—	—	—	—	—	—	7	1.0
<i>Plantago lanceolata</i>	Pl	10	2.2	1	5	2	1	7	1.0
<i>Potentilla erecta</i>	Pe	4	0.9	—	—	1	0.5	35	5.0
<i>Poterium sanguisorba</i>	P	44	10	3	15	23	11	95	13
<i>Prunella vulgaris</i>	Pr	7	1.6	—	—	—	—	1	0.1
<i>Thymus serpyllum</i>	T	46	10	—	—	18	9	25	3
<i>Trifolium repens</i>	Tr	10	2.3	—	—	4	—	—	—
<i>Trisetum flavescens</i>	Tf	—	—	—	—	—	—	12	1.5
<i>Viola hirta</i>	V	3	0.7	2	10	3	1.5	16	2.2
<i>V. silvatica</i>	Vs	—	—	—	—	—	—	3	0.4
Totals		441		20		213		713	

#### MOSSES

<i>Brachythecium purum</i>	%%	<i>Hylocomium triquetrum</i>	••
<i>Camptothecium lutescens</i>	////	<i>Hypnum cuspidatum</i>	
<i>Fissidens taxifolius</i>	\\\\\\	<i>Mnium cuspidatum</i>	≡≡≡

Notes on the frequency of the species on the two areas and within the enclosures.

#### (a) Species characteristic of chalk grassland.

*Festuca ovina*, the most abundant grass of pastured chalk soils, is still locally dominant within the enclosures, though it is decreasing and losing its general dominance as the competition of the other grasses makes itself felt.

*Festuca rubra*, on the other hand, is increasing in both enclosures and is now abundant in A. Possibly it exists outside but has remained undetected.

*Avena pratensis*, another characteristic and abundant chalk grass, but of taller habit, has markedly increased inside both enclosures owing to the withdrawal of rabbit pressure. This increase is more marked on the more calcareous soil of A than on the less calcareous soil of B. *A. pubescens* is absent from A and is apparently decreasing in the B enclosure.

*Trisetum flavescens*, a frequent and very characteristic chalk grass, has not been detected in the Downley area outside the enclosures, and it is only sparingly present within. But the withdrawal of rabbit pressure has evidently given it the chance to develop, perhaps from plants already present which had maintained themselves in the rabbit-eaten turf. Like *Avena pratensis*, it is more frequent in the more chalky soil of the A enclosure.

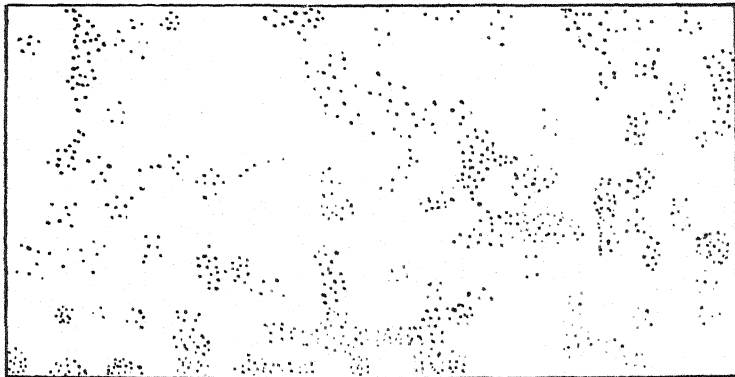


FIG. 7. Distribution of *Festuca ovina* in an area 10 × 5 dm. within the Downley "B" enclosure, Sept. 1920. Scale 1:10.

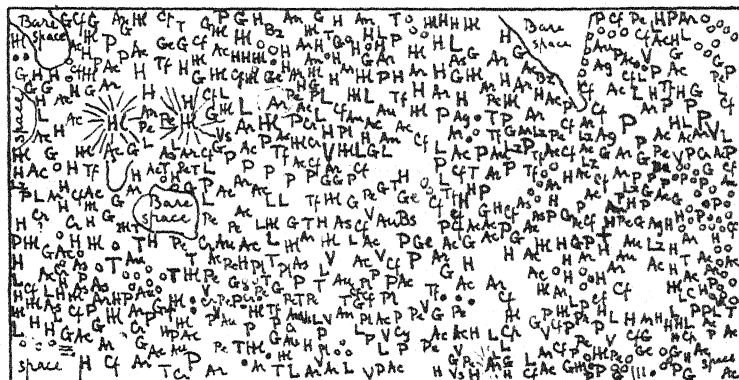


FIG. 8. Plants other than *Festuca ovina* in the same area. Total number of individuals 660. Note the six bare spaces on the soil (all concealed by herbage), the appearance, frequency, and local strength of *Holcus lanatus* and the appearance of *Cynosurus cristatus* (one), *Bromus erectus* (one), and *Brachypodium silvaticum* (one).

*Briza media*, a very widely spread grass of poor dry soils, is apparently decreasing inside the enclosures owing to competition.

*Bromus erectus*, a characteristic dominant of unpastured or only slightly pastured chalk soils, has appeared between 1914 and 1920 in the B enclosure. It is very local in the western region of the South Downs.

*Koeleria gracilis (cristata)* is apparently increasing inside the enclosures.

*Carex flacca (glauca)*, another abundant and characteristic species of chalk



pasture often co-dominant with *Festuca ovina*, is decreasing, though it is still abundant in both enclosures, especially A.

Of the common herbs of chalk soil, *Poterium sanguisorba*, one of the commonest and probably the most characteristic of the abundant species, is maintaining and even increasing its abundance within the enclosures. It forms a much greater percentage of the total weight of the herbage (locally 22.1 against 9.7) and has established local dominance in competition with the grasses.

*Lotus corniculatus* has increased outside with diminished rabbit pressure, but has decreased inside owing to competition.

*Thymus serpyllum*, within the enclosures especially, is tending to become confined to mole heaps. It is distinctly commoner on the more chalky soil of A.

*Scabiosa columbaria* is increasing, apparently with diminished rabbit pressure.

*Hieracium pilosella* and *Gentiana amarella* have quite gone from the B enclosure and almost from the A enclosure.

*Asperula cynanchica*, a low growing species, has apparently disappeared from the B enclosure and has decreased in the A enclosure.

The thistles, *Cirsium acaule* and *C. palustre*, the former of which is very common in chalk grassland as on other dry soils, are both decreasing, as we have already seen, within the enclosures owing to competition. *C. palustre*, generally a plant of wet or stiff soils, is found here and there in chalk grassland, so that it must be reckoned as an occasional member of this community.

*Helianthemum vulgare*, generally reckoned as a very characteristic chalk plant, is absent from A. As a matter of fact, it is scarcely a plant of grassland as such but of chalky spots with open soil. In B it is especially characteristic of mole heaps, and owing to the fewness of these is becoming much restricted inside the enclosure.

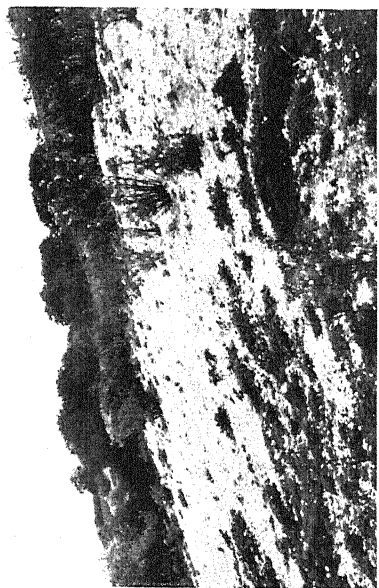
Thus there is a distinctly noticeable tendency for the low growing plants characteristic of chalk pasture to maintain themselves longer in the more chalky soil of the A enclosure. The taller growing species which suffer most markedly from rabbits<sup>1</sup> are increasing within the enclosures, while those which suffer from the competition of taller growing species are decreasing or disappearing altogether.

#### (b) Species not characteristic of chalk grassland.

The species present in the Downley area which are not characteristic of chalk grassland but are commonly found on a wide range of soils or occur more especially on neutral and slightly acid soils, are increasing or decreasing on much the same lines as the more characteristic chalk plants.

Thus *Achillea millefolium* is greatly increasing inside the enclosures,

<sup>1</sup> Cf. Farrow, E. Pickworth "On the Ecology of the Vegetation of Breckland, III. General Effects of Rabbits on the Vegetation." This JOURNAL, 5, 1917, pp. 3 and 16.



Phot. 1. Windmill Hill. Bared area. Mats of *Sedum acre* etc., with *Senecio jacobaea* in foreground, *Atriplex belladonna* behind. Sept. 1920.



Phot. 2. Detail of Phot. 1. *Senecio jacobaea* (right). *Sedum acre* (left). *Arenaria serpyllifolia* (top). Chalk fragments nearly covering soil. Sept. 1920.



Phot. 3. Head of combe south of Oxenbourne Down, Butser Hill. The bare chalk is the result of rabbit devastation. *Tuscium*



Phot. 4. South facing slope of Ramsdean Down, Butser Hill. The half bareness of the slope is not due to rabbit attack; but



evidently because it benefits by withdrawal of rabbit attack and can hold its own in competition with the grasses. *Agrostis tenuis*, on the other hand, is decreasing inside the enclosures apparently owing to competition, perhaps root competition, since it is a shallow rooting species.

Of the other grasses *Anthoxanthum odoratum* is markedly commoner in enclosure B than outside and is absent from A. *Dactylis glomerata* has invaded both enclosures though it is still rare. *Holcus lanatus*, which had invaded B in 1914 is now spreading vigorously and is locally dominant (Plate IV, Fig. 1). *Phleum pratense* and *Brachypodium silvaticum* (the latter primarily a woodland grass) have invaded enclosure B but are still rare. *Rumex acetosa* has also established itself in enclosure B.

*Potentilla erecta* is occasionally met with in chalk grassland where the top layer of soil is poor in lime. It occurs both in A and B, but is distinctly commoner in the latter. In the enclosures however it is barely holding its own in the tall herbage. The greater quantity of soil relatively poor in lime in the former associated with the greater depth of soil, which is generally associated with area. *Scabiosa succisa*, on the other hand, which is generally associated with rather heavy, damp and somewhat acid soils, is unexpectedly present in A and not in B. It has since been found to occur in many other chalk grassland areas.

But one of the most interesting events is the appearance of *Calluna vulgaris* in B enclosure. It occurs in places on the downs, especially on plateaux where there is an upper layer of soil poor in lime, but none has been detected in the pastured Downley Bottom grassland. Five plants of this species were discovered in the B enclosure in 1914, and from their ages had evidently arrived about 1911, probably all at the same time. In 1914 they were all in flower (Pl. IV, Fig. 2). About 1917 some rabbits got into the enclosure and nibbled off the tops of many of the young woody plants, including the *Calluna*. This check to development was not however very serious, and in 1919 the plants had increased in number and were all in flower. In 1920, when the area was again properly surveyed, eight vigorous plants were present, all in flower and holding their own with the grasses. The three new plants were situated close to the old ones and were evidently their seedling offspring. The poverty of the top layer of soil in lime, its distinct acidity, combined with the freedom from rabbit attack inside the enclosure, no doubt accounts for the colonisation of this plot by the ling. The nearest possible seed parents were situated 0.5 and 2.4 km. to the W.S.W. of the plot. The more distant origins of these grassland areas we

To sum up the characteristics and tendencies of these grassland areas we may say that while the B area has always been less typical chalk grassland than A, owing to the less calcareous nature of its soil, the enclosure is rapidly making it still less so by the accumulation of humus, which is leading to a tendency to the gradual replacement of the typical chalk pasture flora by neutral and to a slight extent even a somewhat acid-loving vegetation, though the deep-rooting chalk plants are by no means excluded. But the two inter-

locked factors, viz. absence of grazing and consequent increase of competition, leading to the success of the taller growing plants, appear to be by far the most potent influences in changing the vegetation.

*Marginal woodland species.*

The following marginal herbaceous species are increasing in or invading the enclosures from the edge of the wood, now that rabbit attack has ceased.

*Clinopodium vulgare* local on the wood edge in A area outside enclosure: increasing in B enclosure.

*Fragaria vesca* locally abundant on A outside, increasing somewhat in the enclosure.

*G. mollugo*, invading enclosures, still local.

*Hypericum hirsutum* has invaded B enclosure but is still rare.

*H. perforatum* is increasing somewhat from the wood edge in B enclosure.

*Origanum vulgare*<sup>1</sup>. One plant has recently appeared in B enclosure.

*Potentilla sterilis*, local in A enclosure near wood edge.

*Veronica chamaedrys*<sup>2</sup> and *Viola silvestris*, on the other hand, are apparently decreasing in the enclosures owing to competition in the thick deep herbage.

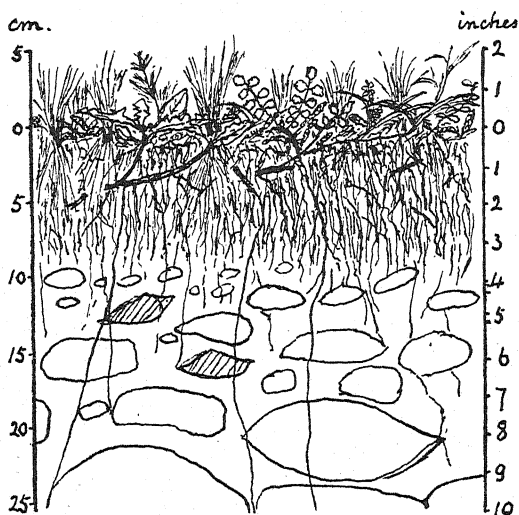


FIG. 9. Downley "B" area (9): profile of herbage and soil outside the enclosure, August, 1914, somewhat diagrammatic. Soil 0-9 cm. firmly held by roots of *Festuca ovina*, *Agrostis tenuis*, *Carex flacca*, *Euphrasia nemorosa*, etc.; 9-20 cm. fine soil mixed with lumps of chalk of all sizes up to 12 cm. diameter (and a few flints) occupying more than half the total volume. Roots of *Poterium* and *Cirsium acaule* extend to at least 25 cm. from surface.

<sup>1</sup> It is doubtful if *Origanum vulgare* is properly placed as a marginal woodland plant. It is characteristic rather of dry chalk banks without thick pastured turf.

<sup>2</sup> *Veronica chamaedrys*, though mainly a wood-edge and "hedge bank" plant, is not very uncommon in chalk grassland.

*Depths of rooting.*

The few very incomplete data on the depths of rooting of ten species which are given below are perhaps worth recording, though they require to be supplemented by much more extended observations in different types of chalk soils. It may be noted however that while two of the four deep-rooting species were holding their own in the Downley "B" enclosure, all six of those with roots of only moderate or shallow penetration are suffering more or less from competition in the enclosures. The contrast in the depths of rooting between these and Weaver's American figures is very striking.

*Depths of rooting in Downley "B" area.*

Deep rooted species		Species with roots of moderate depth		Shallow rooted species	
<i>Cirsium acaule</i>	30 cm.	<i>Asperula cynanchica</i>	11 cm.	<i>Agrostis tenuis</i>	4 cm.
<i>Lotus corniculatus</i>	25 ..	<i>Carex flacca</i>	11 ..	<i>Euphrasia nemorosa</i>	5 ..
<i>Poterium sanguisorba</i>	30 ..	<i>Trifolium pratense</i>	15 ..	<i>Festuca ovina</i>	6 ..
<i>Viola hirta</i>	20 ..				

## E. EFFECT OF DIFFERENT SLOPE EXPOSURES.

The following table shows the occurrence of species on different exposures of War Down and Butser Hill, as well as on two areas of the summit plateau of the former. Chalk *in situ* or chalk lumps occur at a maximum of 10 cm. (4 inches) from the surface of all these areas, and all are more or less rabbit attacked, though some much more severely than others, and the northern part of the summit of War Down (column 5) very little indeed, so that the vegetation is scarcely affected. Comparison of the lists show that difference of exposure has, for the most part, apparently little effect on the occurrence of most species of the chalk grassland community. Steep southern exposures are lacking: from observations in other regions it would seem that they show a restricted list of species. The steep northern exposure of War Down (10), forming part of the escarpment of the Lower Chalk (main chalk escarpment) does however show a marked difference.

This escarpment may reach, in the steepest places, an angle of 34° to the horizon<sup>1</sup>, and a north slope of this steepness cuts off a considerable proportion of the insolation. The preponderance of mosses in many places in the turf of the north escarpment is very noticeable; and they are often definitely dominant over the grasses and herbs. It is the *Hylocomia* which form the bulk of this moss vegetation, as can be seen from the list below, and *H. splendens* is specially prominent. The Downley "A" list (p. 199) should be compared. This area also has a north exposure: its slope is not nearly so steep (17°-18°), but the wood behind on the upper part of the slope cuts off much direct

<sup>1</sup> From comparative observations in the steep sided coombes of Butser Hill, it appears that 37°-38° is the greatest angle at which closely grazed chalk grassland can maintain itself. At 39°-40° there is no continuous turf, but the soil is loose, consisting of small chalk lumps and powdery chalk (lower part of the steep slope shown in Pl. VI, Fig. 4). These observations have since been confirmed in other parts of the southern chalk range.

insolation. At Downley, especially close to the edge of the wood, the *Hylocomia* tend to be dominant (Pl. V, Fig. 3), much more so, for instance, than on Downley B with a more westerly, or on Chalton Peak or Chalton Down with easterly exposures. In the last three areas these mosses, though present, show no tendency to dominance. The same dominance of mosses has been observed in Sussex outside the region considered in this paper, both on the steep northern escarpment and in small areas of chalk grassland existing between and shaded by patches of woodland.

Heavy rabbit attack on a steep northern exposure or otherwise shaded area will tend to increase the dominance of the mosses, since they appear to be refused by rabbits and thus obtain an advantage relatively to the herbs. Thus on a gently inclined north-facing chalk slope in Wiltshire, much infested with rabbits, *Brachythecium purum* and *Hylocomium triquetrum* were found to be generally dominant, with *Thymus serpyllum* and *Helianthemum vulgare* (both relatively rabbit-resistant species) locally dominant, while all other species together formed but a small fraction of the herbage.

The northern slope of War Down increases from 24°, a few metres below the escarpment edge, to 34° some 15 metres lower down the slope. The soil consists of 10 cm. of brown loam, then 20 cm. of chalk lumps mixed with soil, and chalk *in situ* at 30 cm. The herbage averaged 7.5 to 10 cm. in height, an unusual height for a heavily rabbitated area. Mosses were very abundant (15 species of bryophytes occurring) and in places overwhelmingly dominant, isolated shoots of the other plants poking up through the moss carpet, evidently protected by the immune moss. Halfway down the slope (about 40 metres below the area listed) is an aggregation of rabbit burrows and among them a clump of *Sambucus nigra*. Streams of small chalk lumps tailed down the hill from the bushes. The list of species (column 1) contains a fair variety of chalk grassland herbs but with prevailing low frequencies. The grasses particularly fall far behind their usual position in chalk grassland, only four species being detected, and of these only the sheep's fescue was more than occasional. Besides the *Hylocomia*, which are also abundant on the north slope of Butser Hill and on the east of War Down, but not on the other exposures, *Dicranum scoparium* was more abundant than usual, and *Rhacomitrium lanuginosum*, a most unusual moss in this community, occurred locally, as also on the east slope and (abundantly) on the summit plateau, from which last it had probably spread by wind carriage to the north and east slopes.

The southern slopes (11, 17 and 18) were all poor in species, but so were the north slope of Butser Hill (16) and the west slope of War Down (13) and we can scarcely draw conclusions as to the effect of aspect from these data. The list for the east slope of War Down (19) contains by far the greatest number of species, but this is no doubt partly due to the fact that this slope was more thoroughly and persistently explored. It was however undoubtedly richer than the other slopes, and when we remember the richness of Chalton

Down and, to a less extent, of Chalton Peak, which also have eastern exposures, it would almost look as if this was the most favourable aspect for chalk grass-land. Such a conclusion would not be unreasonable when we consider that south and west slopes are more liable to suffer from desiccation, and that on steep north slopes mosses are rather favoured at the expense of flowering plants. But much more extensive observations would be necessary before any certain conclusion could be arrived at.

Table IX. *Soils of War Down (Analysis of air-dry soil).*

Exposure and slope	Depth of sample in cm.	Loss of air-dry soil at 100°	Loss on ignition	Total carbonates as CaCO <sub>3</sub>	CaO	MgO	K <sub>2</sub> O	Insoluble residue	pH
N 30°	2.5-18	6.9	24.4	33.9	21.0	0.3	0.15	29.5	8.0
Summit (N) flat	0-2.5	10.35	42.25	0.76	2.9	0.9	0.18	48.3	6.9
"	2.5-10	9.9	39.0	0.96	3.3	0.9	0.13	47.9	7.6

Table X. *Flora of different exposures on War Down and Butser Hill.*

	War Down										
	Slopes				Summit		Butser Hill				
	N.	S.	E.	W.	N.	S.	N.	S.	S.E.		
	10	11	12	13	14	15	16	17	18		
<i>Achillea millefolium</i>	o.	—	o.	—	o.	l.	o.	—	—		
<i>Agrostis alba</i>	—	—	o.	—	—	—	—	—	—		
<i>A. tenuis</i>	o.	l.a.	a.	—	f.	a.	l.a.	l.	—		
<i>Anthoxanthum odoratum</i>	—	o.	o.	o.	o.	f.	o.	—	—		
<i>Arrhenatherum elatius</i>	—	—	—	—	—	—	a.	—	—		
<i>Asperula cynanchica</i>	f.	f.	f.—a.	f.—a.	f.	f.	f.	f.	a.		
<i>Avena pratensis</i>	o.	—	l.o.	a.	o.	o.	a.	f.	a.		
<i>A. pubescens</i>	—	—	—	—	—	—	o.	—	f.		
<i>Bellis perennis</i>	—	—	o.	—	o.	o.	—	o.	—		
<i>Briza media</i>	—	o.	o.	f.	o.	—	o.	o.	o.		
<i>Calluna vulgaris</i>	—	—	—	—	—	a.	—	—	—		
<i>Campanula rotundifolia</i>	f.	a.	o.—f.	f.	f.—a.	f.	f.	f.	f.		
<i>Carex flacca</i>	a.—v.a.	a.	v.a.	a.	v.a.	a.	v.a.	v.a.	a.		
<i>C. praecox</i>	o.	o.	o.	o.	f.	l.a.	—	r.	l.a.		
<i>Carlina vulgaris</i>	—	o.	o.	l.f.	—	o.	—	—	o.		
<i>Cerastium vulgatum</i>	o.	—	o.	—	o.	—	—	—	—		
<i>Cirsium acaule</i>	f.	a.	f.—v.a.	a.	a.	l.a.	o.	f.	a.		
<i>C. lanceolatum</i>	l.	—	r.	—	—	—	r.	—	—		
<i>C. palustre</i>	—	—	—	—	—	—	r.	—	—		
<i>Clinopodium vulgare</i>	—	—	r.	—	—	—	—	—	—		
<i>Cynoglossum officinale</i>	—	—	—	—	—	—	r.	—	—		
<i>Cynosurus cristatus</i>	—	f.	a.	—	—	—	—	—	—		
<i>Dactylis glomerata</i>	r.	—	l.	—	—	—	—	—	—		
<i>Daucus carota</i>	—	—	—	o.	—	—	—	—	—		
<i>Euphrasia nemorosa</i>	—	o.	o.—f.	l.	f.	o.	—	o.	—		
<i>Festuca ovina</i>	v.a.	v.a.	v.a.—d.	a.	v.a.—d.	a.	d.	d.	d.		
<i>Galium erectum</i>	l.	—	l.	—	—	—	—	r.	—		
<i>G. verum</i>	o.	—	o.	—	—	f.	—	o.	—		
<i>Gentiana amarella</i>	o.	—	r.—o.	r.	—	—	—	—	—		
<i>Hieracium pilosella</i>	l.a.	—	l.a.	a.	a.	o.	—	—	l.		
<i>Holcus lanatus</i>	—	—	—	—	—	o.	—	—	—		
<i>Leontodon autumnalis</i>	o.	f.	o.—a.	—	o.	f.	—	—	o.		
<i>L. hispidus</i>	o.	—	f.—a.	a.	o.	f.	—	o.	o.		
<i>Linum catharticum</i>	f.	o.	o.—f.	f.	f.	f.	f.	—	a.		
<i>Lolium perenne</i>	—	—	l.	—	—	—	—	—	—		
<i>Lotus corniculatus</i>	v.a.	f.—l.a.	a.	f.	a.	a.	o.	a.	a.		
<i>Medicago lupulina</i>	—	—	—	—	—	—	o.	o.	—		



Table X (continued).

	War Down								
	Slopes				Summit		Butser Hill		
	N. 10	S. 11	E. 12	W. 13	N. 14	S. 15	N. 16	S. 17	S.E. 18
<i>Myosotis arvensis</i>	l.	—	l.	—	—	—	—	—	—
<i>Phleum pratense</i>	—	—	o.	—	—	—	—	—	—
<i>Phyteuma orbiculare</i>	—	—	l.	—	—	—	—	—	—
<i>Pimpinella saxifraga</i>	—	—	o.	—	—	—	—	—	—
<i>Plantago lanceolata</i>	o.—f.	—	f.—a.	f.	o.	f.	—	f.	—
<i>P. media</i>	—	—	l.o.	—	—	—	—	o.	—
<i>Polygala vulgaris</i>	—	o.	o.	o.	o.	—	—	o.	o.
<i>Potentilla erecta</i>	—	—	—	—	—	o.	—	—	—
<i>Poterium sanguisorba</i>	—	—	—	—	—	—	—	s.d.	—
<i>Primula veris</i>	o.	—	r.—o.	—	—	—	—	r.	—
<i>Prunella vulgaris</i>	o.	f.	o.—f.	—	—	—	f.	f.	o.
<i>Ranunculus bulbosus</i>	r.	o.	o.	o.	—	—	o.	o.	o.
<i>R. repens</i>	—	—	r.	—	—	—	—	—	—
<i>Rumex acetosa</i>	o.	—	o.	—	—	—	—	—	—
<i>Scabiosa columbaria</i>	—	—	o.	—	—	—	—	—	—
<i>S. succisa</i>	—	—	l.a.	—	—	—	—	—	—
<i>Senecio jacobaea</i>	o.	o.	o.	—	o.	r.	f.	o.	o.
<i>Taraxacum erythrospermum</i>	—	—	—	—	—	—	r.	—	r.
<i>Thymus serpyllum</i>	a.	a.	a.	a.	a.	a.	a.	a.	a.
<i>Trifolium pratense</i>	—	—	o.—f.	l.	—	o.	—	—	—
<i>T. repens</i>	o.	o.	o.—l.	—	—	o.	—	—	—
<i>Trisetum flavescens</i>	—	f.	—	f.	—	—	—	—	—
<i>Urtica dioica</i>	l.	—	r.l.	—	—	—	—	—	—
<i>Veronica arvensis</i>	l.	—	r.	—	—	—	—	—	—
<i>V. chamaedrys</i>	o.	—	o.	—	o.	—	o.	o.	—
<i>V. officinalis</i>	—	—	—	—	—	—	o.	—	—
<i>Viola hirta</i>	l.a.	o.	f.—l.a.	—	—	—	—	—	f.
<i>V. riviniana</i>	o.	—	o.	—	—	l.a.	o.	—	—
Totals	34	23	52	23	24	28	26	26	22
<i>Cornus sanguinea</i>	—	r.	—	—	—	—	—	—	—
<i>Juniperus communis</i>	—	o.	—	—	—	—	—	—	—
<i>Rosa canina</i>	—	—	r.	—	—	—	—	—	—
Totals		2	1						
<i>Brachythecium purum</i>	a.	f	a.	f.	a.	a.	f.	f.	a.
<i>Camptothecium lutescens</i>	a.	f.	a.	f.	a.	f.	—	a.	a.
<i>Dicranum scoparium</i>	a.—v.a.	l.a.	a.	l.	a.	a.	f.	—	—
<i>Fissidens adiantoides</i>	o.	—	o.	—	—	—	—	r.	—
<i>F. taxifolius</i>	—	—	—	o.	—	—	—	—	—
<i>Hylocomium splendens</i>	v.a.—l.d.	—	l.d.	—	o.	l.	a.	—	—
<i>H. squarrosum</i>	a.—l.d.	—	a.—l.d.	—	—	—	f.	—	—
<i>H. triquetrum</i>	a.	—	a.	o.	o.	o.	a.	a.	—
<i>Hypnum chrysophyllum</i>	—	—	o.	—	—	—	—	—	—
<i>H. cupressiforme v. elatum</i>	f.	—	f.	—	f.	—	—	—	—
<i>H. cuspidatum</i>	o.	—	o.	—	—	—	—	—	—
<i>H. molluscum</i>	a.	—	f.—a.	o.	—	—	—	f.	f.
<i>Neckera crispa</i>	o.	—	o.—f.	l.a.	—	—	—	o.	a.
<i>Rhacomitrium lanuginosum</i>	l.	—	l.	—	l.a.	—	—	—	—
<i>Thuidium abietinum</i>	f.	o.	f.	—	—	o.	o.	—	—
<i>T. tamarascinum</i>	o.	—	o.	—	—	—	—	—	—
<i>Trichostomum tortuosum</i>	—	—	—	—	—	—	o.	—	f.
<i>Frullania tamarisci</i>	l.a.	—	o.—l.a.	—	l.a.	—	—	—	—
<i>Cladonia fimbriata</i>	—	f.—l.a.	l.a.	f.	v.a.	l.	l.	—	f.
<i>C. furcata</i>	—	—	—	—	v.a.	l.	—	—	—
<i>C. silvatica</i>	—	—	—	—	v.a.	l.	—	—	—
<i>Peltigera canina</i>	—	—	o.	—	—	—	—	—	o.
Totals	15	5	18	8	11	9	8	6	7
90 species in all	49	30	71	32	35	37	34	32	29

The two summit areas listed (14 and 15), separated by about 600 metres, show floras which on the whole correspond pretty closely—a rather poor chalk grassland flora with an admixture of other elements, the local abundance of *Rhacomitrium* on the former (800 feet) and of *Calluna* on the latter (700 feet alt.) being the most noticeable floristic difference. The turf of the latter area is more compact owing to more persistent rabbit nibbling, and it contains a few extra grassland species, such as the two *Trifolia*, *Galium verum*, *Holcus lanatus*, *Potentilla erecta* and *Viola riviniana*, while the former has more bryophytes and lichens. The high lying summit of War Down, fully exposed to the prevailing moisture-laden south-westerly winds, would doubtless show a specially high rainfall and relative humidity during the frequent weather periods of south-westerly type.

The soils of these two flat areas appear to be similar, chalk lumps occurring at no great depth—4 inches in one and 3½ inches in the other area.

#### F. THE EFFECT OF RABBITS.

It appears that the excessive multiplication of rabbits in certain places on the Downs has only taken place within comparatively recent years, and that it is mainly the result of definite preservation or the formation of rabbit warrens for purposes of sport. The occurrence of rabbits in great numbers is in fact quite local, and the animals do not normally travel far in search of food even when it has become exceedingly scarce in the immediate neighbourhood of their burrows. Thus at a distance of 150 to 200 yards from a large aggregation of burrows, round which for some yards the vegetation is completely destroyed, there is little sign of rabbit attack. As they multiply, of course, the animals have to go further for their food, but they never go further than they need<sup>1</sup>.

The incidence of rabbit pressure on the vegetation thus varies from place to place, and also from time to time, as the rabbits are preserved or are systematically trapped. Shooting alone does not effect more than a temporary reduction in their numbers.

The herbage of a good sheep pasture, not too heavily grazed, varies according to soil and water content from about 2 to 4 inches (5 to 10 cm.) in height. Anything like heavy rabbit attack reduces the herbage to a height of ½"–1" (or say 1 to 2·5 cm.), and ruins the pasturage for sheep. Sheep and cattle of course eat off the seedlings of woody plants, but they do not commonly graze right up to bushes, so that in the near neighbourhood of these the herbage grows taller and woody seedlings may establish themselves.

This is apparently often the cause of the frequent alternation on common grazing land of clumps of bushes with closely grazed pasture. If some bushes have established themselves at a time when pasturage is in abeyance or is insignificant, they will continue to grow and increase

<sup>1</sup> Cf. Farrow, E. P. On the zonation of vegetation round rabbit burrows in Breckland. This JOURNAL, 5, 1917, pp. 10–16.

by the formation of clumps round the original bushes in spite of grazing, though they cannot colonise the area generally. Thus the sharp alternation between two different types of vegetation originates and is maintained. An example of this has been observed adjoining an old neglected plantation on Cissbury Hill in the central Downs of Sussex. In 1885 an area here was covered with rough herbage among which were numerous young plants of *Ulex europaeus* and *Ligustrum vulgare* (l.d.) with *Crataegus monogyna*, *Prunus spinosa* and *Ilex aquifolium*. Thirty-five years later this area bore dense clumps of bushes 2 or 3 metres high, consisting of these species with *Viburnum lantana*, *Sambucus nigra*, *Rubus* spp. and *Lonicera periclymenum*. Between the clumps were tracts of pure, fairly closely grazed grassland. Close round each clump was taller herbage with some woody seedlings. This is a good example of local differentiation through the action of the biotic factor. It is noteworthy that the bulk of the woody vegetation was spinose, and all but one species had fleshy fruits, i.e. were probably bird sown.

But in a heavily rabbit-attacked area the rabbits not only shave the herbage close to the ground but nibble the bushes themselves up to the height they can reach. The edge of scrub or woodland in such an area has a characteristic clean cut appearance with a sharp lower limit to the foliage of the bushes, about 18 inches (45 cm.) above the ground, and bare soil under and immediately round the shrubs, a glance at which at once betrays the presence of rabbits in great numbers.

It does not appear that moderately heavy rabbit attack has much effect on the floristic composition of chalk pasture, though it makes the establishment of woody plants completely impossible. A sample of a rabbit infested area shows much the same list of species as one in which rabbits are scarce or absent. A comparison of the lists on pp. 196-199 outside and inside the Downley enclosures will show the plants which do not exist, or are at least very hard to find on a rabbit attacked area, but which appear within a few years when rabbits (and other grazing) are excluded. The competition of the new comers, however, soon alters the balance of the vegetation, apart altogether from the arrival of woody plants.

On steep northern exposures and other places shaded from direct insolation the existence of heavy rabbit attack does however alter the vegetation very markedly, as already described on p. 208. Here mosses are generally especially prominent in the herbage, and these the rabbits appear to neglect altogether, while nibbling down the flowering plants. The result is that the mosses, especially the *Hylocomia*, become dominant, though a variety of the common chalk grasses and herbs maintain themselves, protected by the tufts and carpets of moss, through which their shoots grow. This is well seen in the list (p. 210) from the steep northern escarpment of War Down, and it is also seen on the Downley "A" area close to the edge of the wood, as well as in other places in Sussex on the main escarpment of the Lower Chalk.

There are also a certain number of flowering plants normally refused by rabbits, but none of these appears to be a constant constituent of chalk grassland, though some occur here and there. On the flat or gently sloping summit of Holt Down for instance (20), where neither soil nor flora is that of a chalk down (see list on p. 219), there is a large area of rabbit warren, and

in this most of the herbage is very severely eaten down. The following species were found to be untouched: *Senecio jacobaea*, *Glechoma hederacea*, *Teucrium scorodonia* (these three were the commonest untouched plants); *Urtica dioica*, *Verbascum thapsus*, *Erythraea centaurium*, *Cynoglossum officinale*, *Cirsium arvense*, *C. lanceolatum*<sup>1</sup>. Of the chalk grassland "constants" *Thymus serpyllum* seems to be relatively immune, and probably *Cirsium acaule*.

When rabbit attack is very heavy indeed, however, the flora is impoverished, and, especially on fairly steep slopes, the soil is opened to erosion, the vegetation being completely destroyed. This normally happens immediately around the burrow complexes on a hillside, but more extensive examples were seen on the east slopes of War Down, in the eastern coombes of the Butser Hill *massif* (Pl. VI, Fig. 3), and on the north side of Windmill Hill (near Chalton) (Pl. VI, Figs. 1 and 2). The last case was examined in some detail.

*Windmill Hill* (19). Even on the upper part of the north slope of this hill, where the declivity is not more than 12° or 15°, a great deal of soil is thus exposed, more than half the area in many places being completely bared. Moles (*Talpa europea*) add to the destruction by turning up loose soil mixed with lumps of chalk from the subsoil, and the rain washes the earthy constituents away and disintegrates the chalk, so that the surface becomes covered, largely or entirely, with small chalk fragments<sup>2</sup>. The bare white patches thus formed show up on the hillside from a great distance away.

Lower down the hillside, where the slope is steeper (20°–25°), an area 30 m. × 15 m. round a collection of burrows is entirely covered with this loose chalk. Scattered in this were plants of *Urtica dioica*, *Senecio jacobaea* and *Atropa belladonna*, standing up tall and conspicuous from the bare chalk, and nearly all quite untouched by rabbits (Pl. VI, Fig. 1). A few plants of the Deadly Nightshade were badly attacked, some of the stems being half gnawed through, and a few of the Ragworts were also nibbled. Here and there were a few scattered plants of *Sedum acre*, *Arenaria serpyllifolia* (Pl. VI, Fig. 2), *Cerastium vulgatum* and *Myosotis arvensis*, all quite untouched. A little to the east of this completely bare area is a steep-sided coombe with the degenerate remnant of an old beechwood. Here also the soil is practically naked over an acre or so of the valley side, though with a more numerous flora of scattered plants—all rabbit attacked except *Urtica dioica* and *Solanum dulcamara*.

The following lists illustrate the degeneration of the vegetation as a result of the rabbit attack. The first gives the species occurring on a typical area of two square metres near the top of the hill, with a very slight slope to the north, at a distance of perhaps 80 metres from the nearest rabbit burrow complex. The turf is very heavily rabbit-eaten, the herbage not exceeding 2 cm. in

<sup>1</sup> Farrow, *op. cit.* p. 8, gives *Solanum nigrum*, *Conium maculatum*, *Urtica dioica*, and *U. urens* as the only plants he found completely untouched in the rabbit warren on Cavenham Heath in Breckland.

<sup>2</sup> It would be interesting to determine whether abundance of moles is often correlated with abundance of rabbits, as it seems to be in this area, and, if so, the causes of the correlation.

height, but still continuous. Only eight species of flowering plants occurred on this small area:

<i>Agrostis tenuis</i>	r.	<i>Prunella vulgaris</i>	f.
<i>Euphrasia nemorosa</i>	r.	<i>Ranunculus bulbosus</i>	o.
<i>Festuca ovina</i>	a.	<i>Taraxacum erythrospermum</i>	o.
<i>Lotus corniculatus</i>	a.	<i>Thymus serpyllum</i>	f.

In the immediate neighbourhood there were, in addition, *Senecio jacobaea*, *Helianthemum vulgare* (l.d.) (known to be usually refused by rabbits), *Galium verum* and *G. erectum* (believed to be relatively unpalatable). This is of course an exceedingly poor flora for chalk grassland even when rabbit eaten. For instance there were 30 species of flowering plants on one square metre of the Downley "B" area in 1914, and 24 on two square metres of the north-east slope of War Down in the same year—both areas considerably rabbit eaten, while on the most severely rabbit-eaten slope of Butser Hill (herbage 1.5–2.5 cm.) there were 22 species of flowering plants on 12 square metres, which would certainly give more than eight species on two square metres, though it shows the nearest approach to the Windmill Hill conditions.

The soil was comparable in depth with that of the "primitive" chalk grassland near Buriton Limeworks (*a*, p. 184) but was different in nature. The top 1½ inches (3.75 cm.) was a brown loam (D 2), densely matted with roots. Below this was 2 inches (5 cm.) of similar loam (D 1) mixed with small chalk lumps, resting on partly disintegrated chalk *in situ* with brown soil in the fissures.

Table XI. *Analysis of Windmill Hill soil.*

	D 2	D 1		D 2	D 1
	0–3.75 cm.	3.75–8.75 cm.		0–3.75 cm.	3.75–8.75 cm.
(0–1.5 inches) (1.5–3.5 in.)					
Water lost on air drying	27.4	24.2	K <sub>2</sub> O	.425	.300
Water lost at 100° C.	6.4	4.7	MgO	.500	.092
Loss on ignition	7.27	31.4	CaO	20.30	26.12
Total carbonates	36.2	44.0	Insoluble residue	32.6	23.0
Nitrates as NaNO <sub>3</sub>	.0067	.0038	"Lime require- ment"	Nil	.015
P <sub>2</sub> O <sub>5</sub>	.312	.178			

Though still a highly calcareous soil, with a distinctly high lime content in the top 1½ inches, this is decidedly more leached and contains more humus than the Buriton Limeworks "*a*" soil, and it is noteworthy that its humus content is much greater in the lower layers. It is probably an older soil, belonging to a later stage in the succession than the Buriton Limeworks "*a*" soil, and we can only suppose that its surface layers have been impoverished in humus by persistent severe rabbit-attack diminishing the supply of humus-forming material. The presence of *Agrostis tenuis* and *Prunella vulgaris*, in spite of the very small number of species, probably mark the difference of age. Figs. 10 and 11 show profiles of this herbage and soil. The diminution in size of the plants and their parts, and the shallowness of the general rooting are seen to be very marked if Fig. 10 is compared with Figs. 2 and 9, which are drawn to the same scale.

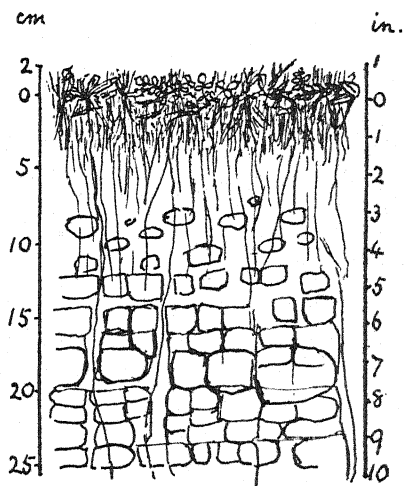


FIG. 10.

Fig. 10. Windmill Hill (19), profile of herbage and soil in very severely rabbit-eaten area, Sept. 1920, somewhat diagrammatic. Herbage under 2 cm. high. *Festuca ovina*, *Lotus corniculatus*, *Thymus serpyllum*, *Plantago lanceolata*, *Prunella vulgaris* etc.; 0-4 cm. brown loam densely matted with roots; 4-9 cm. soil mixed with chalk lumps.

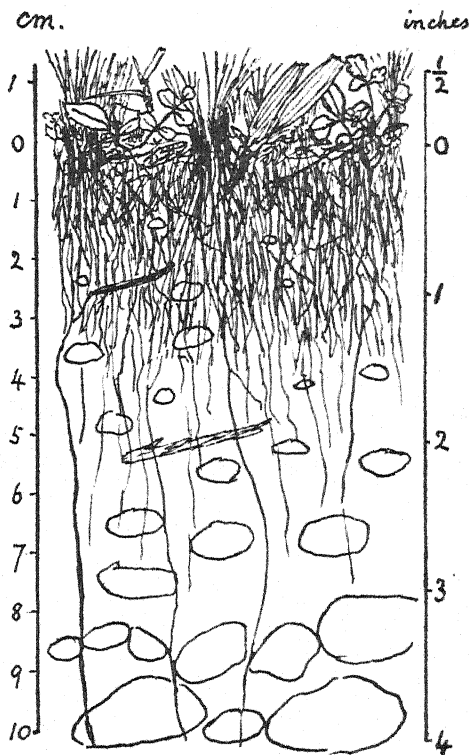


FIG. 11.

Fig. 11. Windmill Hill, profile of herbage and soil, drawn on a larger scale, from another spot under the same general conditions. Chalk lumps stop spade at 10 cm.

Note the great reduction in the size of the shoots and leaves and the shallow general root stratum as compared with Figs. 2 and 9.

Passing now to the semi-bare areas nearer the rabbit burrow complexes, we find a sharp differentiation between the flora of the islands of turf and that of the loose soil bared by the action of the rabbits and moles.

(1) *Species occurring in turf still remaining.*

<i>Agrostis tenuis</i>	o.	<i>Hieracium pilosella</i>	l.
<i>Anthoxanthum odoratum</i>	o.	<i>Holcus lanatus</i>	o.
<i>Asperula cynanchica</i>	f.	<i>Lotus corniculatus</i>	f.
<i>Campanula rotundifolia</i>	o.	<i>Plantago lanceolata</i>	o.
<i>Cerastium vulgatum</i>	o.	<i>Poterium sanguisorba</i>	r.
<i>Cirsium palustre</i>	o.	<i>Taraxacum erythrospermum</i>	o.
<i>Euphrasia nemorosa</i>	o.	<i>T. officinale</i>	r.
<i>Festuca ovina</i>	l.—l.d.	<i>Thymus serpyllum</i>	f.
<i>Galium erectum</i>	o.	<i>Veronica chamaedrys</i>	f.
<i>G. verum</i>	o.	<i>Viola riviniana</i>	r.
<i>Helianthemum vulgare</i>	l.a.—l.d.		

## (1) Species occurring in turf still remaining (continued)

## BRYOPHYTES

*Camptothecium lutescens	l.a.	*Hypnum molluscum	f.
Brachythecium purum	l.a.		
Fissidens taxifolius	o.	Lophocolea bidentata	o.
Hylocomium triquetrum	o.		

## (2) Bryophytes in disintegrated turf on margins of turf "islands."

*Barbula cylindrica	o.	*Hypnum chrysophyllum	l.a.—l.d.
B. fallax	o.	*H. molluscum	l.f.
Bryum pallens	r.	Polytrichum piliferum	o.
*Ditrichum flexicaule	l.a.	†Tortula ruralis	l.f.

## (3) Species on bare soil with chalk lumps partially covering loam.

Arenaria serpyllifolia	v.a.	Rumex acetosa	f.
Atropa belladonna	o.	Sambucus nigra	r.
Cerastium semidecandrum	o.	Sedum acre	v.a.
C. vulgatum	o.	Senecio jacobaea	a.
Cirsium lanceolatum	o.	S. vulgaris	r.
Cynoglossum officinale	r.	Sonchus asper	o.
Myosotis arvensis	f.	Urtica dioica	l.
Reseda luteola	r.	Veronica arvensis	o.

\* Calcicole.

† Slightly preferring lime, according to Watson.

Of these three distinct communities (1) the turf plants show an impoverished list of a fairly advanced chalk pasture, but with some open soil species, and a marked poverty in grasses, (2) the disintegrated margins of the turf islands bear a collection of mosses which include a proportion of calciphilous species, but of which *Polytrichum piliferum* usually at least occurs on non-calcareous soil, while (3) the bare soil shows a scattered collection of plants none of which is a constant constituent of chalk grassland, though a few occasionally occur in it. Most of these plants which had colonised the bare soil were quite untouched by the rabbits. The conspicuous feature was the abundance of *Arenaria serpyllifolia* and *Sedum acre*.

Figs. 12 to 15 represent the root systems of isolated plants on the bare soil described. There is a suggestion of two strata of maximum root absorption,

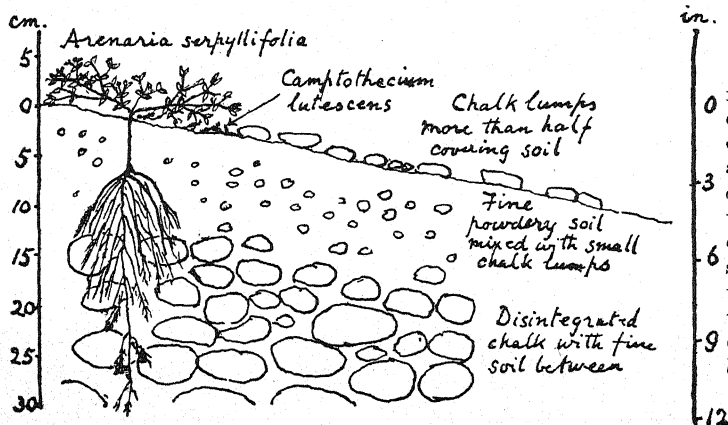


FIG. 12. Windmill Hill, profile of area destitute of turf. Slope about 15°. *Arenaria serpyllifolia* with vertically descending root system with active rootlets at 10 to 30 cm., and *Camptothecium lutescens*.

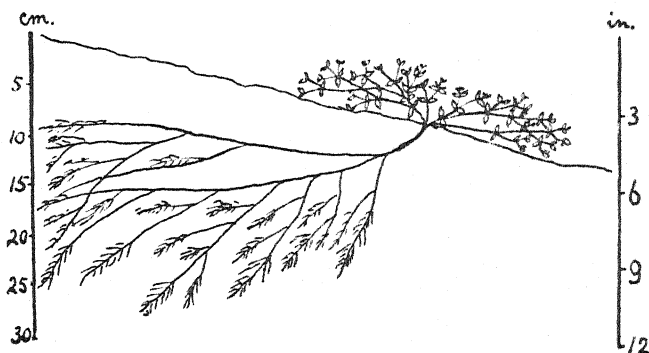


FIG. 13. Another plant of *A. serpyllifolia* from same area, but with root system laterally displaced and pointing uphill: active rootlets at 10 to 25 cm.

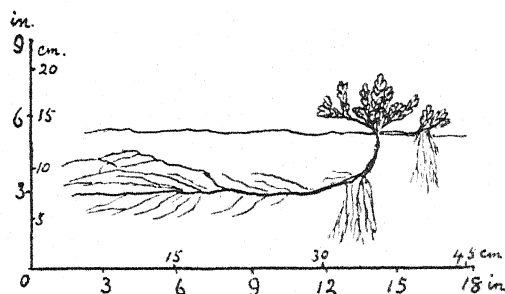


FIG. 14. Windmill Hill. *Sedum acre* on bare area, with laterally displaced root system, horizontally directed; also vertical bunches of roots: active rootlets 2-10 cm. from surface.

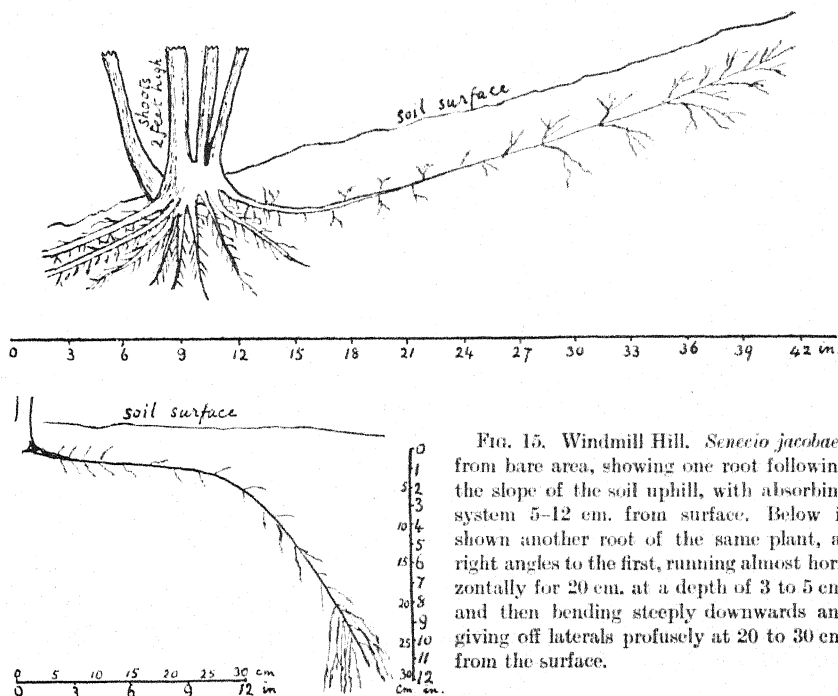


FIG. 15. Windmill Hill. *Senecio jacobaea* from bare area, showing one root following the slope of the soil uphill, with absorbing system 5-12 cm. from surface. Below is shown another root of the same plant, at right angles to the first, running almost horizontally for 20 cm. at a depth of 3 to 5 cm. and then bending steeply downwards and giving off laterals profusely at 20 to 30 cm. from the surface.



one at about 2 to 6 inches, the other at 8 to 12 inches and over (Fig. 15, lower drawing), but the data are not sufficient to enable any safe conclusion to be drawn. Figs. 13 and 15 (upper drawing) also suggest that the main stem or stock of the plant has been forced down the slope (which might be quite possible in the loose, powdery soil), and that the roots "left behind" have afterwards developed further in the surface layer, horizontally or at a slight angle below (Fig. 13) or above (Fig. 15) the horizontal. But again the data are insufficient and the direction of root development may be determined entirely by the distribution of water supply.

On the steep (east-facing) slope of the adjoining coombe there was no turf, and large tracts of soil were covered with chalk fragments quite bare of plants. The following flowering plants occurred: no bryophytes were met with.

<i>Anagallis arvensis</i>	o.	<i>Plantago media</i>	l.
<i>Arctium minus</i>	f.	<i>Reseda luteola</i>	o.
<i>Arenaria serpyllifolia</i>	l.a.	<i>Sambucus nigra</i>	l.f.
<i>Asperula cynanchica</i>	l.	<i>Sedum acre</i>	f.—l.a.
<i>Atropa belladonna</i>	o.	<i>Senecio jacobaea</i>	f.
<i>Campanula glomerata</i>	r.	<i>Solanum dulcamara</i>	l.a.
<i>Cirsium lanceolatum</i>	o.	<i>Sonchus asper</i>	o.
<i>C. palustre</i>	o.	<i>S. oleraceus</i>	o.
<i>Festuca ovina</i>	l.	<i>Taraxacum officinale</i>	r.
<i>Galium erectum</i>	r.	<i>Teucrium scorodonia</i>	l.
<i>G. verum</i>	r.	<i>Urtica dioica</i>	f.—l.a.
<i>Helianthemum vulgare</i>	l.a.	<i>Verbascum nigrum</i>	l.
<i>Leontodon autumnalis</i>	r.	<i>V. thapsus</i>	l.
<i>Myosotis arvensis</i>	f.		

Here, in addition to a few chalk pasture species, there are a majority of open soil plants, ten of which occur in the last list, the relative abundance of *Arenaria serpyllifolia* and *Sedum acre* again being noticeable. *Urtica dioica* and *Solanum dulcamara* were the only two species absolutely untouched by rabbits.

The occurrence of *Teucrium scorodonia* is interesting. This plant has rather the reputation of being a calcifuge and doubtless the immense majority of individuals of the species in this country occur in light soils very poor in lime, but here it grows on soil containing an enormous proportion of calcium carbonate. Nor is this an isolated instance. In a similar heavily rabbit-attacked locality on Butser Hill it grows in sheets rooted in practically pure chalk, and it has been observed in the same habitat elsewhere on the South Downs. It is also a characteristic species on dry rocky limestone slopes in the ashwoods of Derbyshire and West Yorks.

#### G. GRASSLAND ON DEEPER NON-CALCAREOUS SOIL OVERLYING THE CHALK.

The soil of the Downley "B" area is a good example of a comparatively shallow soil (8 inches = 20 cm.) overlying chalk, which shows the effect of leaching and humus formation in a marked degree. The arrival of *Calluna*, in fact, suggests the formation of a chalk heath, though the advance of woodland would quickly overtake it. It has been shown by one of us (Adamson, *l.c.*) that the plateau and dipslope of the chalk in this region bears a series of woods whose vegetation reflects the increased depth of non-calcareous soil very closely. The Downley "A" grassland corresponds with Adamson's "Beech-

woods on Chalk" and "Calcareous Coppice" (Watt's "sere 4"), the "B" grassland with Adamson's "Transition Coppice" and "Plateau Beechwood" (Watt's "sere 3").

The grasslands of the deeper, relatively non-calcareous, soils overlying the chalk have not been given much attention, but it may be interesting to add lists of the vegetation of two such areas: (20) the extensive flat summit of Holt Down (alt. 500 feet) which is used as a rabbit warren and the vegetation of which is severely eaten down (see p. 213); and (21) an area of grassland in the valley between Holt Down and Windmill Hill, which is pastured but not severely rabbit eaten. Both are deep loam soils relatively poor in lime, the latter (21) consisting of 10 to 12 inches (25-30 cm.) of uniform light brown loam showing the following constitution:

*Valley grassland, (21) sample 0-12", uniform light brown loam  
without chalk lumps.*

Loss on air drying	27.0	K <sub>2</sub> O	323
Loss at 100° C.	4.7	MgO	291
Loss on ignition	69.0	CaO	3.21
Total carbonates	4.3	Insoluble residue	67.0
Nitrates as NaNO <sub>3</sub>	.0045	"Lime requirement"	.10
P <sub>2</sub> O <sub>5</sub>	.170		

It will be seen that this closely resembles the Downley "B" soils, but with markedly less carbonates and markedly more humus, this fraction being as high as in many woodlands. The area is evidently an old pasture not impoverished by rabbit attack.

Table XII. *Lists of flora, Holt Down (20) and adjacent valley (21).*

	20	21		20	21
Achillea millefolium	o.	a.	Potentilla erecta	f.—a.	a.
Agrostis tenuis	v.a.—d. a.—v.a.		Prunella vulgaris	o.	o.
Anthoxanthum odoratum	a.	a.	Ranunculus bulbosus	—	o.
Bellis perennis	—	o.	Sagina procumbens	o.	—
Calluna vulgaris	l.	l.	Senecio jacobaea	f.	f.
Campanula glomerata	—	f.—a.	Taraxacum officinale	o.	—
C. rotundifolia	a.	—	Thymus serpyllum	o.	l.a.
Carduus nutans	—	l.	Trifolium pratense	—	o.
Carex caryophylla	—	f.	T. repens	a.	a.
Cerastium vulgatum	—	r.	Veronica arvensis	o.	—
Cirsium acaule	—	o.	V. chamaedrys	o.	—
C. arvense	o.	—	V. officinalis	o.	—
C. lanceolatum	—	o.	Viola riviniana	f.—l.a.	—
C. palustre	o.	f.			
Cynosurus cristatus	—	f.	Totals	28	29
Euphrasia nemorosa	o.	—			
Festuca ovina	v.a.	a.	BRYOPHYTES		
Galium saxatile	l.a.	—	Brachythecium purum	o.	f.
G. verum	f.	f.	Dicranum scoparium	o.	l.a.
Hieracium pilosella	—	o.	H. squarrosum	a.	f.
Holcus lanatus	l.a.	l.a.	H. triquetrum	—	f.
Leontodon autumnalis	o.	o.	Hypnum cupressiforme		
Leucanthemum vulgare	o.	—	var. elatum	—	o.
Lotus corniculatus	f.	f.—a.	Polytrichum gracile	o.	—
Luzula campestris	a.	o.	P. piliferum	l.	—
Plantago lanceolata	f.	a.			
P. media	—	r.	Totals	5	5
			48 species in all.	Totals	33
					34

The grassland of both areas was interspersed with clumps of bushes in which yew and hawthorn were prominent. Oak-hazel wood existed in the immediate neighbourhood.

An examination of the lists shows that the herbage differs markedly from that of typical chalk grassland, the closest resemblance being to that of the Downley "B" area, but there are fewer "chalk plants." *Festuca ovina*, though still abundant, yields pride of place to *Agrostis tenuis*. The ubiquitous sedge of chalk pasture, *C. flacca*, is absent, the Avenae are absent, while *Anthoxanthum* and *Holcus lanatus* and *Trifolium repens* are abundant: *Potentilla erecta* is abundant and *Galium saxatile* appears. The mosses are few, but include two species of *Polytrichum* on the Holt Down area. The lists in fact are not "chalk grassland" lists at all.

### 3. SUMMARY.

Selected representative samples of stages in the colonisation of bare chalk and of pasture grassland on the chalk soils of the western end of the South Downs are described. The region covered lies due south of the town of Petersfield and extends about three miles from east to west and about four miles from north to south. It includes the outcrops of the Lower, Middle and Upper Chalk, and bears a considerable extent of woodland (mainly beech) and a moderate amount of arable land, in addition to the pasture grassland.

1. The only plants found establishing themselves on the actual surface of living chalk in the only locality studied were the moss *Seligeria calcarea* and a species of *Chroolepus* (A, p. 180). Various flowering plants can settle in the cracks of exposed chalk. The colonisation of quarry talus and spoil surfaces was examined, and these were found to be colonised by a varied collection of plants, mainly open soil pioneers and chalk grassland species where the bare surfaces are surrounded by grassland, but including a miscellaneous collection of weeds and marginal woodland plants where arable land and woodland exist in the vicinity. *Festuca ovina* and *Carex flacca* are prominent colonists on fine spoil surfaces, together with *Tussilago farfara* locally, and the moss *Camptothecium lutescens* (B, pp. 180-183).

2. The various areas of chalk grassland examined are described roughly in the order of "succession." First three very small patches of "primitive" grassland (A, pp. 183-186) which illustrate the increase in depth and variety of the herbage accompanying decrease in carbonate content of the soil with increase of soil depth, humus and water content; then areas of well developed typical chalk pasture (B, pp. 186-189) with a deeper soil (the surface layer of which is poor in lime) and a much greater variety of plants; then an area of "wasteland" (C, pp. 189-190) into the colonisation of which marginal woodland plants as well as grassland species largely enter; and finally an area (Downley Bottom) in which rabbit-proof enclosures were constructed, so that the effect of the exclusion of this factor (and of all grazing) could be followed

(D, pp. 190–206) as shown by changes both in the vegetation and in the soil.

Additional lists of species are given from different slope exposures of War Down and Butser Hill, as well as from the summit plateau of the former (E, pp. 206–211); the effect of steep northern exposures, particularly in conjunction with heavy rabbit attack, on the balance between moss and phanerogamic vegetation is brought out.

The effects of rabbit attack on the vegetation (widespread and heavy in this region) are then dealt with generally (F, pp. 211–213) and a particular severely attacked area (Windmill Hill) is studied in some detail (pp. 213–218).

Finally lists of the species occurring in two areas of grassland on deep soil overlying chalk, but containing only a moderate amount of lime, one rabbit-eaten and one not, are given (G, pp. 218–220) and compared with those of chalk grassland.

#### 4. CONCLUSIONS.

The general conclusions are very much what might have been expected from the more or less vague knowledge we already possessed.

The first significant colonisation of bare chalk is by “chomophytes,” not “lithophytes.” A wide variety of species can colonise chalk talus and particularly finely divided chalk débris, and which do so depends largely on the surrounding vegetation. When chalk grasslands surround the bare area *Festuca ovina* comes at once to the fore, and remains, in this region, the typical dominant or co-dominant of pastured chalk grassland. Mosses play a fairly prominent part from an early stage, but the first colonists are different (largely calcicole) species from the later ones (largely *Brachythecium purum*, and in shaded places species of *Hylacomia*), which remain constant constituents of mature grassland. In “primitive” grassland, i.e. when the soil is shallow and contains a very high percentage of carbonates, and little humus even in the superficial layer, the variety of species is small and these, both flowering plants and mosses, are of xerophilous type.

With increasing depth of soil and increasing humus and water-content a much greater variety of herbaceous species appears, and the typical richness of the chalk grassland community is developed. *Festuca ovina* remains dominant or co-dominant with *Carex flacca*, or at least very abundant, equalling or exceeding any other species in quantity. Of other grasses *Avena pratensis* is the commonest, with *Trisetum flavescens* and *Avena pubescens* usually less common. *Bromus erectus* is rare and local in this region. *Briza media* is occasional but pretty widely distributed. This condition is maintained so long as the land is moderately grazed. The herbage varies from 2–4 inches (5–10 cm.) in height according to grazing and water content.

Moderately heavy rabbit attack reduces the general height of the herbage to one inch (2.5 cm.) or less, but does not effect any great change in the list

of species present, though it injures some species more than others and thus relatively favours the resistant species. But on the whole the species of chalk grassland, being hemicryptophytes, are able to withstand rabbit attack as well as sheep grazing. On steep northern exposures, and where the vegetation is otherwise shaded, mosses, especially the *Hylocomia*, are very abundant, and here heavy rabbit attack at once gives the moss vegetation dominance, reducing the phanerogamic vegetation to a subordinate position.

Very heavy rabbit attack which stops short of baring the soil does however appear greatly to reduce the number of species. Exactly how this happens has not been determined. To obtain an answer to the question it would be necessary to study the behaviour of an area of grassland rich in species from the time when it was first exposed to the attack.

Except immediately around burrows, where scratching is an additional factor preventing the maintenance of vegetation, it is especially though not exclusively on fairly steep slopes that the ground is extensively bared by rabbits, especially when aided by moles. Loose soil together with chalk lumps is brought up and the soil is washed down the slope by rain, leaving the surface covered, partially or entirely, by loose fragments of chalk. Such areas are in part completely bare of plants, but are tenanted here and there by species which rabbits do not touch or only occasionally bite. The root relations of these are interesting.

In the absence of rabbit pressure and with not too heavy grazing there is a tendency to the invasion of chalk grassland by plants not characteristic of it. This is the result of increasing depth of soil, both by dissolution of chalk below and by the accumulation of humus above, together with the washing out of carbonates from the surface layers. Some of these plants are species which have a distributional mode on acid soils, such for instance as *Potentilla erecta* and *Calluna vulgaris*. Of the grasses there are shallow rooted forms like *Agrostis vulgaris*, which cannot be called characteristic of typical chalk grassland, though it is often present and sometimes abundant, and *Holcus lanatus*, which is very local, though where this grass appears it often becomes locally dominant. More important are the deeper rooted grasses which increase in, or invade chalk pasture whose soil is deep. The Avenae, which appear when the soil is still shallow, increase notably, often at the expense of *Festuca ovina*, when the soil deepens and grazing is not severe, but in this region *Avena pratensis* rarely approaches dominance, as it does for instance in enclosure A (the one with the most chalky soil) at Downley. On the central and eastern downs, where the plague of rabbits is not nearly so widespread and severe the dominance or co-dominance of *Avena pratensis* is much commoner, though of the taller growing grasses, *Bromus erectus* (very local on the western downs) is the typical dominant in the east. *Trisetum flavescens* is widespread but rarely very abundant and never dominant. *Dactylis glomerata*, while by no means a characteristic chalk grassland species,

is a fairly constant member of the herbage except on the shallowest soils. The other meadow grasses play little part in this region, and no areas have been met with such as those which often occur on the central and eastern downs, especially on the north-facing escarpment, where a considerable number of species of tall grasses, those already mentioned, *Festuca rubra*, *Poa pratensis*, *Arrhenatherum elatius*, *Deschampsia caespitosa*, and even *Festuca elatior*, alternate or compete for dominance, accompanied by diminution or disappearance of many of the lower growing species of the typical sheep's fescue chalk pasture. This is doubtless to be correlated with a much more restricted occurrence of rabbits in the central and eastern regions. The western area, part of which is dealt with in this paper, is a region of large estates with extensive woodlands, maintained primarily for the amenities of their owners, and with relatively little agricultural land. The centre and east are regions of farms, where rabbits are not encouraged, and the extensive grasslands are treated as an integral part of the farm system.

NOTE. The soil analyses, the expenses of which were defrayed by Royal Society grants, were carried out partly at the Cambridge School of Agriculture and partly by Messrs Waterfall and O'Brien, of Bristol. It should be noted that they are analyses of single samples only, and have therefore only the value of such determinations.

# HALOPHYTEN- UND XEROPHYTEN-STUDIEN.

VON BORIS KELLER.

(Voronesh, Russland.)

(Mit 11 Figuren im Text.)

Unweit von Voronesh liegt das grosse Gebiet des sogenannten Süd-Osten Russlands, wo die Landwirtschaft einen hartnäckigen Kampf um die Vergrösserung ihres Areals und die Vermehrung des Ertrags zu führen hat. Unübersehbare Landstriche, ansehnliche Staaten von West-Europa an Grösse weit übertreffend, sind von der Landwirtschaftlichen Kultur fast unberührt, und bieten zur Zeit nur ein dürftiges Auskommen einer Nomadenbevölkerung dar. In diesem Grenzgebiete, wo die europäische Landwirtschaft den Wüsten Asiens nahe kommt, ereignen sich oft trockene Jahre, in welchen die Missernten den Charakter wahren Katastrophen annehmen.

Es giebt zwei Gründe, die der schablonmässigen Landwirtschaft, an welche unsere Bevölkerung gewöhnt ist, in ihrem Drange nach Süd-Osten eine Grenze setzen: die Dürre des Klimas und des Bodens, und auch der öfters beobachtete, mehr- oder weniger ansehnliche Salzgehalt des letzteren.

Eine bedeutende und bahnbrechende Arbeit steht der russischen Agromie in dieser Hinsicht vor; verschiedene Wege sind schon vorgezeichnet, auf deren Besprechen wir aber uns nicht einlassen können. Wir setzen uns das Ziel, denjenigen von diesen Wegen ausführlich zu beleuchten, welchen wir in den beiden an der Grenze des Süd-Ostens gelegenen, in engstem Kontakte mit einander arbeitenden Versuchs-Anstalten, der Pflanzen-ökologischen Versuchstation bei der Landwirtschaftlichen Hochschule in Voronesh und der Abteilung für angewandte Botanik der Regionalen Versuchstation zu Voronesh ausgearbeitet haben.

Diejenige Gesamtheit unserer Forschungen, welche das Thema dieser Arbeit bildet, war durch die folgende Idee geleitet: um die geeigneten Kulturpflanzen ausfindig zu machen, und ihr Bestehen an die Bedingungen einer verhältnissmässigen Dürre und hohen Salzgehalts des Bodens anzupassen, ist es notwendig die Lebensverhältnisse der wilden Pflanzen sich vor Augen zu stellen. Das Studium der Oekologie wilder Pflanzen wird uns Anweisungen für die Kulturpflanzen geben. Wir müssen deshalb untersuchen, wie die Oekologie der letzteren und auch die Eigentümlichkeiten ihrer Form, ihres Baues, ihrer Lebensäusserungen seien sollen, um solche Pflanzen für unsere Ziele nutzbar zu machen. Wir haben schon ein umfangreiches Material über

Pflanzenassoziationen der trockenen Bezirke Russlands (sogenannte Halbwüsten und Wüsten) zu unserer Verfügung und tief eindringende Beobachtungen in diesem Gebiete: die Pflanzenassoziationen sind schon in verschiedenen Zeiten ihrer Vegetationsperiode beschrieben, Bodenanalysen ausgeführt, die Verteilung der Wurzelsysteme in verschiedenen Bodenhorizonten, wie auch der osmotische Druck in den Assimilationsorganen untersucht worden u.s.w. Das Vorhandensein des letztgenannten Materials ist eine Vorbedingung um sich durch eine eingehende Analyse der Pflanzenassoziationen die charakteristischen ökologischen Pflanzentypen für ein monographisches Studium auszuwählen. Die ausgewählten Pflanzen sollen monographisch studiert werden, da wir besonderen Wert auf die Wechselbeziehung der Pflanzenmerkmale legen, um die Pflanze als einen physiologische Maschine zu betrachten. Die Natur hat nämlich mehrere Lösungen für dasselbe ökologische Problem. Wenn man, zum Beispiel, wie es gewöhnlich in der Literatur auftritt, die diversen Merkmale verschiedener Xerophyten zusammenstellt, so ist es dasselbe, als ob man Teile der Maschinen, die wohl einem Zwecke dienen, aber verschieden gebaut sind, auf einen Haufen wirft.

Im Folgenden sind in einer sehr gedrängten Form einige Ergebnisse unserer Arbeit angegeben.

#### I. UNTERSUCHUNGEN ÜBER DAS HALOPHYTGLASSCHMALZ "SALICORNIA HERBACEA L."

Im Süd-Osten sind solche Salzböden verbreitet, deren starker Salzgehalt (meistens an  $\text{NaCl}$  und  $\text{Na}_2\text{SO}_4$ ) mit einer intensiven Befeuchtung (durch nahes Grundwasser oder Landseewasser) selbst während der Sommerhitze zusammenrifft. Es ist ein sehr störender Umstand für die Landwirtschaft im trockenen Süd-Osten, dass in denjenigen kleinen Localitäten, wo Wasserfülle herrscht, auch eine starke Salzhaltigkeit stattfindet.

Für solche stark ausgeprägte Salzböden sind die folgenden zwei starken Halophytentypen charakteristisch:

- (a) sukkulente Salzpflanzen, die eine grosse Menge leichtlöslicher Salze in ihrem Zellsafte anhäufen:
- (b) nicht sukkulente Pflanzen, welche bedeutende Quanta derselben Salze ausscheiden.

Zum monographischen Studium war das Glasschmalz (*Salicornia herbacea* L.) als ein hervorragender Vertreter des ersten Typus erwählt. Die Pflanze erscheint in vielen Fällen als ein Vorläufer der höheren Pflanzen in salzreichen Böden. Selbst erfahrene Beobachter müssen öfters die kleine Pflanze bewundern, welche ihr Leben in einem mit starken Salzlösungen getränktem Boden fristet, wenngleich weit minder konzentrierte Lösungen auf gewöhnlichen Pflanzen schon tödlich wirken.

Das Glasschmalz hat schon die Aufmerksamkeit vieler Forscher auf sich gelenkt und die Literatur enthält darüber recht zahlreiche Anweisungen.



Tabelle I. Die Transpirationsintensität in ihrer Abhängigkeit vom Grade der Versalzung.

In den Kolonnen A ist der gesamte Wasserverlust für die ganze Periode in Gramm, in den Kolonnen B—das Mittel pro Tag für eine Pflanze in Milligramm pro Quadr. Cent. der Oberfläche angegeben; für den Atrometer—in Gramm, ohne Bezug zu der Oberfläche.

Nummern und Serien	Gehalt an NaCl	8 Tage 21-28. vii.		3 Tage 26-28. vii.		6 Tage 29. vii.-3. viii.		3 Tage 1-3. viii.		3 Tage 8-10. viii.		1 Tag 26. vii.		1 Tag 28. vii.		3 Tage 23-25. viii.		Gehalt an NaCl
		A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	
Kulturen zwei Serien a) ein jedes b) ein jedes enthält 8 % Nähr- ung und ein anular Glas- malz	1 a)	23.1 180	185.5	10.2 150	152.5	46.6 243	248	29.3 234	239	29.5 125	136	5.0 221	216.5	2.2 97	98	—	—	—
	2 a)	30.9 191	191	13.6 155	155	64.1 253	253	40.3 244	239	50.6 147	136	6.2 212	212	2.9 99	99	—	—	—
	3 a)	28.2 164	164	12.9 136	136	65.8 206	209	42.7 190	193.5	57.9 108	100.5	5.8 184	184	3.2 101	101	—	—	123
	4 b)	—	—	5.9 147	137.7	26.4 212	212	16.7 197	193.5	18.8 98	98	2.6 194	194.3	1.4 104	104	—	—	57
	5 b)	—	—	4.0 130	130	—	—	—	—	—	—	2.1 205	205	0.9 88	88	—	—	—
	6 a)	11.6 134	130	4.9 109	109	22.2 160	165	14.3 183	183	18.9 90	90	2.2 145	145	1.2 79	79	—	—	40
Kulturen, denen eine 0.85 Gramm. 2 Gramm. ein er- hat, und Exemplare Glaschmalz t	7 b)	8.7 126	126	2.9 104	104.5	15.8 170	165	9.8 168	168	12.2 86	86	1.3 140	137.7	0.5 54	54	—	—	26
	8 a)	—	—	3.5 98	98	—	—	—	—	—	—	1.6 136	136	0.7 59	59	—	—	5
	9 b)	—	—	3.3 95	95	—	—	—	—	—	—	1.5 130	130	0.6 52	52	—	—	19
	10	Nicht zu-	—	17.1 155	155	63.3 235	232.5	36.0 242	242	—	—	6.5 240	238	3.9 144	146.5	—	—	—
	11	gesetzt	—	21.3 155	155	81.7 230	230	45.6 218	218	—	—	7.9 236	236	5.0 149	149	78	78	—
	12	2 Gramm. ein	—	50.8 104	104	215.9 166	162	118.1 141	141	—	—	18.6 161	161	12.5 108	108	—	—	—
Exemplare Glaschmalz	13	Mal zuge-	—	53.1 101	102.5	213.9 158	162	111.1 132	136.5	—	—	19.5 156	156	13.2 106	107	39	39	—
	14	setzt	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Wie bei 12 u. 13 und noch begos- sen mit 1 % Lösung NaCl	15	u. 13 und	—	22.4 62	57	99.0 90	88	55.4 82	73.5	—	—	8.2 95	85.5	5.8 69	66.5	15	15	—
	16	noch begos-	—	20.6 52	52	79.5 77	77	43.6 65	65	—	—	6.9 76	76	5.8 64	64	—	—	—

Atmometer

Dennoch ist die Lebensart dieser merkwürdigen Pflanze noch wenig beleuchtet; die zu unserem Gebote stehenden Versuche sind sehr ungenügend, und ein treffendes Bild des Lebens der *Salicornia herbacea* L. ist nicht zu entwerfen.

Wir führen die Ergebnisse unserer Versuche über das Glasschmalz (im Jahre 1919 ausgeführt) auf dieser Stelle an.

### 1. DIE TRANSPIRATION UND DIE AUSTROCKNUNG.

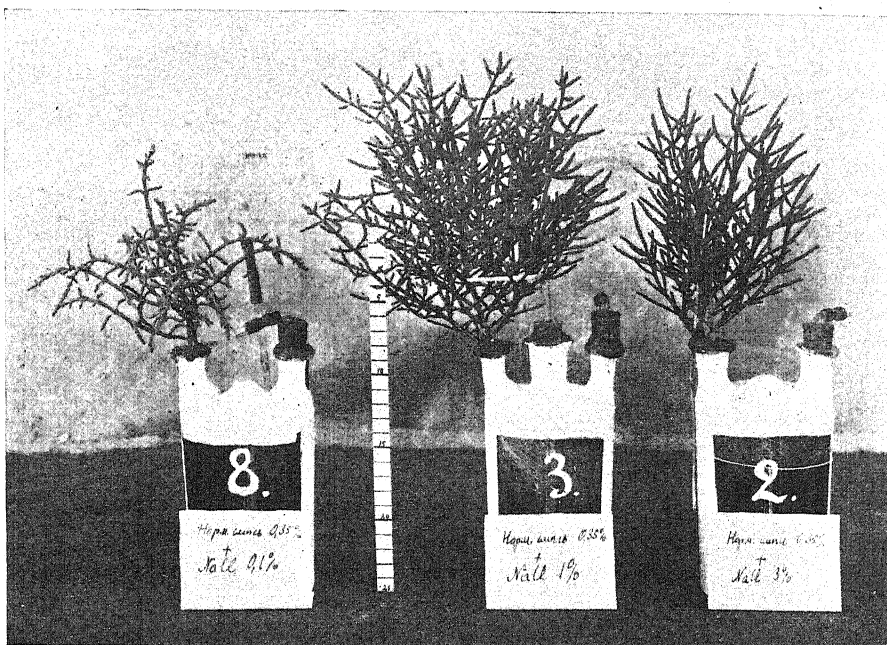
E. M. Delf hat bereits gezeigt, dass die Verdunstung auf die Einheit der Oberfläche bezogen bei dem Glasschmalz sehr gross ist, und z. B. diejenige der *Vicia cracca* übertrifft. Hier tritt schon die alte Frage auf ob es nach der Ansicht von Schimper eine Verwandtschaft zwischen den Xerophyten und den Halophyten besteht, oder ob, nach den entgegengesetzten extremen Ausführungen z. B. Chermezons, den echten Halophyten die Merkmale der Xerophyten in den meisten Fällen fremd sind.

Unsere Aufgabe bestand darin die Eigentümlichkeiten der Transpiration bei dem Glasschmalz und ihre Abhängigkeit von der Anwesenheit und dem Grade der Versalzung zu beleuchten, zu gleicher Zeit aber auch festzustellen, ob die Pflanze sich gegen das Austrocknen genügend zu schützen vermag. Die Ergebnisse sind in den folgenden 5 Tabellen zusammengestellt; die nötigen Erklärungen sind in den Bemerkungen zu einer jeden Tabelle angegeben. Ausführliche Angaben über die Aufstellung der Versuche mit der *Salicornia herbacea*, von denen hier die Rede ist, sind in einer von meinen Arbeiten in russischer Sprache enthalten. (Siehe auch Fig. 1.)

Zu Tabelle I. Die absolute Grösse der Transpiration pro Tag für die verschiedenen Exemplare während der ersten Periode war unbedeutend; deshalb sind nur die Mittelwerte für 6–8, resp. 3 Tage angegeben. In zwei Fällen sind jedoch Angaben für einen Tag angeführt, wobei zwei naheliegende, im Wetter stark differierende Tage ausgewählt waren; der 26. vii.—ein heisser sonniger, und der 28. vii.—ein stark bewölkter, kühler Regentag. Am 31. viii. war es schon möglich die Daten für einen einzigen Tag zu benutzen. Die Pflanzen waren damals am höchsten Punkte ihrer Vegetationsentwicklung, und gingen zu dem nächsten Lebensstadium, der Blütezeit, über; einige Pflanzen waren schon aufgeblüht.

Zu Tabelle III. Der Versuch war mit Pflanzen von denselben Wasserkulturen, wie die in den Versuchen für die Tabellen I und II, ausgeführt.

Zu Tabelle IV. Für die Versuche waren Pflanzen von denselben Sandkulturen, wie für die Versuche zu Tabelle I gebraucht. Um die Geschwindigkeit der Austrocknung der Typen einer jeden Kultur zu ermitteln waren je 2 Exemplare des Glasschmalzes in voller Entwicklung abgeschnitten (diese Exemplare sind mit römischen Ziffern bezeichnet); zum Vergleich war die Transpirationsintensität der nicht abgeschnittenen Pflanzen derselben Kulturen ermittelt (gewöhnliche Ziffern).

FIG. 1. *Salicornia herbacea* L., Wasserkulturen.

8 = 2a in der Tabelle I.

3 = 3a „ „

2 = 6a „ „

Tabelle II. Die Transpirationsintensität für dieselben Wasserkulturen, wie in Tabelle I (in Gramm auf 100 Cub. Cent. vom Volumen der assimilierenden Triebe berechnet).

Nummern und Serien der Gefässe	Der Gehalt an NaCl %	Das Mittel pro Tag für Periode 21-28. vii.	Das Mittel pro Tag für Periode 29. vii.-3. viii.	Das Total für 14 Tage von 21. vii.-3. viii. auf 100 Cub. Cent. des endlich. Volumen berechnet	Der Gehalt an NaCl %	Für den Tag 31. viii.	
1 a)	0.1	467	445	3060	—	—	
2 a)		500	472	3200			
3 a)	1	409	337	2000	1	194	
4 b)			384	360		258	
6 a)	3	322	324	2330	3	150	
7 b)		318	309	2240		138	
8 a)						127	
9 b)		315	294	2150		5	114

## Die Versuchsergebnisse.

1. Diejenigen Pflanzen, die ohne Versalzung erzogen waren, welche also kein Chlornatrium empfangen, oder welchen diese Substanz in kleiner Konzentration beigebracht wurde, zeigten eine hohe und, was auch zu bemerken ist, eine gleiche Transpirationsintensität.

Tabelle III. *Der tägliche Gang der Transpiration.*

	Gefäß- nummern	Gehalt an NaCl %	30. viii. 7	31 August									31. viii. 7
			U. n. M. - 31. viii. 7 U. v. M.	7-8½ U. v. M.	8½-10	10-11½	11½-1	1-2½	2½-4	4-5½	5½-7 U. n. M.	1. ix. 7 U. v. M.	
Wasserkulturen. Ein jedes Gefäß enthält 0.38 % Nährsalz- lösung und ein Ex- emplar des Glas- schmalzes	3 4 6 7 8 9	1  3 5	48.3 47 30.8 37.5 20 22.2	29.6 27 30.8 30 33.3 21.6	60 54 63.5 61.2 63.3 47.3	98.6 91 90.4 88.7 80 91.4	100 100 100 100 100 100	91 89 86.7 97.2 86.5 86.2	65.3 64 59.2 60 66.7 58.3	33.3 36 25 25 13.3 27.8	18.5 20 13.5 13.7 3.3 16.7	58.6 52 36.5 40 30 33.3	
Der Atmometer			193.9	21.6	47.3	81.8	100	92.6	74.3	54.1	37.2	155.4	
Der Photometer von Stenstrup (die An- zahl der kleinen Lichtpünktchen)			—	14	16	19-20	19	18	15-16	11	8	—	
Der Psychrometer von Ass- mann (die Zahlen sind für die Zeiten der Wägung an- gegeben)		t° nach C Relative Feuchtig- keit	23.1-18.2 61-60	22.4 58	26.5 45	29.2 30	29.8 50	27.8 46	26.9 47	24.4 50	22.2 64	19 63	

Tabelle IV

*Die Austrocknung und teilweise (zur Vergleichung) die Transpirationsintensität bei den in verschiedenen Graden der Versalzung gezogenen Pflanzen.*

Die Anfangszeit des Versuches		Die Nummern der für das Aus- trocknen abgeschnittenen Exem- plare (römische Ziffern) und der Gefäße mit Glasschmalz für die Transpirationsmessungen (ge- wöhnliche Ziffern)	Bemerk. über NaCl-Gehalt im Substrat: "nichts" - kein NaCl- gehalt; "mittel" - auf ein Gefäß 2 Gramm NaCl einmal zugesetzt; "gross" - wie im vorhergehenden + Begossen mit 1 % Lösung von NaCl	Der Wasserverlust									
				in Milligrammen pro 1 Quadr. Cent. Fläche in		in Prozenten zu dem Anfangsgewicht in							
				den ersten 40 Min.		den ersten 40 Min.		1 St. 20 Min.	2 St. 40 Min.	24 St.	48 St.	96 St.	
2. viii.	I			—	9.5	—	28.5	40	60	81.4	84.2	84.7	
9 U. 50	II	nichts	—	11.7	10.6	—	30.5	45.8	66.1	84.5	89.8	90.2	
I. vor M.	III			—	8.7	—	22.9	36.7	57.1	80	89.2	90.2	
	IV	mittel	—	9.8	9.2	—	23.7	36.3	57.8	82.3	90.5	91.9	
	V			—	5.7	—	13.1	21.7	35.9	53.9	66.6	87.5	
	VI	gross	—	5.9	5.8	—	15	22.5	37.5	57.6	71.7	89.4	
	11	nichts	—	—	13.6								
	13	mittel	—	—	11.9								
	14	gross	—	—	7.3								
9. viii.	VII			den ersten 25 Min.	den ersten 50 Min.	den ersten 25 Min.	den ersten 50 Min.	1 St. 15 Min.	2 St. 30 Min.	24 St.	48 St.	96 St.	
U. v. M.	VIII	nichts	—	3.3	4	12.1	14.5	16.1	19.5	38.2	55.5	68.2	
	IX			3.8	4.3	11.8	13.5	14.7	15	35.3	54.1	66.5	
	X	mittel	—	2.5	3	5.6	6.9	8.2	11.3	23.8	33.5	43.9	
	XI			2.4	3.1	5.0	6.5	8.4	11.4	24.3	34.4	43.2	
	XII	gross	—	0.6	0.8	1.6	2.1	3.3	5.6	15.6	21.7	29.1	
				0.3	0.5	0.9	1.3	2.5	4.8	15.7	22.0	28.4	
27. viii.	XIII			den ersten 25 Min.	den ersten 50 Min.	den ersten 25 Min.	den ersten 50 Min.	1 St. 15 Min.	2 St. 30 Min.	24 St.	48 St.	96 St.	
10 U. 50	XIV	nichts	—	5.1	7.2	14.1	21.6	26.4	37.6	46.9	58.7	77.6	
V. v. M.	XV			6.2	11.8	9.5	13.8	26.2	29.7	39.3	51.7	67.6	
	XVI	mittel	—	3.8	6.8	8.8	15.8	19.7	30.5	35.4	43.6	59.3	
	XVII			4	7.6	9.2	17.8	22.7	31.5	37.1	44.6	59.5	
	XVIII	gross	—	1.3	3.1	2.8	6.8	8.6	14.8	20	25.6	36.6	
				1.4	3.3	3.2	7.2	9.1	15.2	20.2	25.8	36.1	
	11	nichts	—	—	11.7								
	13	mittel	—	—	4.5								
	14	gross	—	—	2.1								

2. Diese Intensität wird vermindert, wenn die Konzentration des NaCl anwächst; und wird bei sehr starker Salzhaltigkeit ganz unbedeutend; sie bleibt aber noch ziemlich hoch bei 1 % von NaCl in Wasserkultur.

3. Die Transpirationsintensität wird vermindert sich zur Blütenzeit. Es muss jedoch bemerkt werden, dass, von dem ökologischen Standpunkte aus, die Periode der vegetativen Entwicklung und des Wachstums, wenn die Pflanze gegen das Austrocknen am wenigsten geschützt ist, wohl die grösste Bedeutung haben muss. Auch hat das Glasschmalz die Neigung zu einer späteren, nämlich zu der Fruchtzeit, ihre assimilierende und transpirierende Oberfläche zu vermindern, durch das Abwelken der saftigen Glieder am unteren Teile der Pflanze beginnend.

4. Tabelle II zeigt an, wie das Glasschmalz bei seiner Transpiration sich mit der Einnahme eines sehr geringen Quantum von Chlornatrium aus den starken, ihre Wurzel umgebenden Lösungen, begnügt. In der Tat, bei einer Kultur mit einer 3-prozentigen Lösung von NaCl hat das Glasschmalz gegen das Ende einer zweiwöchentlichen Periode 2240 gr. Wasser auf 100 Cub. Cent. seines Volumen verdunstet. Wenn eine solche Lösung von der Pflanze unmittelbar eingeatmet würde, so müsste der Gehalt an NaCl im Körper der Pflanze zu der unmöglichen Höhe von 70 Gr., oder 70 % steigen. In Wirklichkeit, nach der Steigung des osmotischen Druckes beurteilt, hat das Glasschmalz höchstens nur 1–2 Gr. von NaCl auf 100 Cub. Cent. seines Volumen eingenommen; was nur 1–2 % anstatt 70 % ausmacht.

5. Selbst mit einer 5 % Lösung von Chlornatrium zeigt das Glasschmalz einen regelmässigen Gang der täglichen Transpiration. Die Transpirationskurve ist der Kurve derjenigen Pflanze, die mit 1 % NaCl gezogen war, sehr ähnlich. Als einziger Unterschied, tritt die Verminderung der Nachttranspiration mit der Vergrösserung des Gehaltes von NaCl hervor.

6. Die von den Wurzeln abgetrennten, assimilierenden Triebe des Glasschmalzes, zeigen bei dem Austrocknen dieselben charakteristischen Verschiedenheiten, wie bei der Transpiration: die Pflanzen, die ohne Salz gezogen waren, verlieren die Feuchtigkeit, im Vergleich mit den Pflanzen der versalzten Kulturen, wesentlich schneller. Dieser Unterschied zeigt sich sowohl in den ersten Minuten des Trocknens, als auch in der nachfolgenden längeren Zeit.

7. Wenn man überlegt, dass bei dem mit normaler Nährstofflösung gezogenem Glasschmalz der Wassergehalt bemerkenswert geringer ist, so liegt es auf der Hand, dass das Wasser bei dem Austrocknen dieser Pflanzen und auch bei der Transpiration viel sparsamer verbraucht wird, als bei den mit einem Zusatz von Salz gezogenen Exemplaren.

8. Es ist bemerkenswert, dass in den ersten Minuten das Austrocknen (auf die Einheit der Fläche berechnet) und die Transpirationsintensität augenscheinlich sehr nahe aneinander liegen. So war es z. B. an einem sehr heissen Tage, dem 2. viii., für eine ziemlich lange Periode von 40 Minuten.

Es wäre natürlich besser eine kürzere Periode von etwa 15 Min. anzunehmen, leider aber konnte man dabei keiner exakten Wägung der Zinkgefässe sicher sein.

9. Es lässt sich nach dem Vorhergegangenen wohl behaupten, dass die bei einem Zusatz von NaCl gezogene Pflanzen im Vergleich mit denen, die ohne Salz gezogen waren, in ihren assimilierenden Trieben eine weit grössere Resistenz gegen die Dürre im Sinne der Fähigkeit dem austrocknenden Einfluss der Umgebung entgegen zu wirken, besitzen.

10. Man ersieht aus Tabelle IV, dass die von stark versalzten Kulturen stammenden Exemplare der *Salicornia*, welche besonders widerstandsfähig gegen die Austrocknung waren, auch einen hohen osmotischen Druck aufweisen; es ist leicht denkbar, dass dieser Druck wohl eben der Grund ihrer Resistenzfähigkeit, sein musste. Da wird die schon besprochene Abwesenheit entsprechender Vorrichtungen in der Epidermis und die Lage der Spaltöffnungen leicht verständlich. Man muss auch nicht ausser Acht lassen, dass durch den Einfluss von Salz die *Salicornia* Veränderungen in ihrer Form und ihrem Bau erhält; wir erinnern nur an solche Veränderungen, die schon längst in der Literatur bemerkt waren (Batalin, Lesage u. a.)—eine starke Entwicklung der Sukkulenz und speciell die Entwicklung derjenigen Gewebe, die das Wasser anhäufen, sowie auch die Verminderung der Spaltöffnungen pro Flächeneinheit.

## 2. DIE ENTWICKLUNG DES GLASSCHMALZES IN IHRER ABHÄNGIGKEIT VON DEM GRADE UND DER ART DER VERSALZUNG.

Für diese Frage finden sich Berichte über Versuche von Batalin, A. Halket u. a., aber die Ergebnisse dieser Versuche sind nicht ganz im Einklange miteinander; manchmal wäre auch eine tiefere Bearbeitung und eine grössere Bestimmtheit derselben zu wünschen.

Die Ergebnisse unserer Versuche sind in den Tabellen VI–VIII kurz zusammengestellt. (Siehe auch Fig. 2–5.)

Tabelle V. *Quantitative Charakteristik der typischen Exemplare von Sandkulturen. (Aus einem jedem Gefäss ein Exemplar entnommen.)*

Gefässnummern	Gehalt an Salz im Gefäss, abgesehen von der normalen Nährstofflösung	Gewicht im frischen Zustande in Gr.	Die oberirdischen Teile				Gefässnummern	Gehalt an Salz im Gefäss, abgesehen von der normalen Nährstofflösung	Gewicht im frischen Zustande in Gr.	Die oberirdischen Teile			
			Gesamte Länge in Cent.	Fläche in Quadr. Cent.	Volumen in Cub. Cent.	Verhältnis der Fläche zu dem Volumen				Gesamte Länge in Cent.	Fläche in Quadr. Cent.	Volumen in Cub. Cent.	Verhältnis der Fläche zu dem Volumen
31	nur Normal-lösung	1-12	96-3	32-9	0-99	33-2	—	—	—	—	—	—	—
4	+ NaCl 1 Gr.	5-16	311-7	148-7	5-96	24-9	16	+ KCl 1-3 Gr.	4-87	291-1	134-3	5-43	24-7
24	+ Na <sub>2</sub> SO <sub>4</sub> 24-3 Gr.	9-70	490-7	242-9	10-45	23-2	27	+ KCl 29-8 Gr.	1-93	107-2	47-9	1-82	26-3
5	+ NaCl 10 Gr.	16-22	677-7	365-3	16-9	21-6	18	+ KCl 12-8 Gr.	3-70	162-8	84-9	4-18	20-3
11	+ NaCl 30 Gr.	5-62	123-6	121-0	9-89	12-2	20	+ KCl 38-4 Gr.	1-19	40-6	26-8	1-46	18-4
14	+ NaCl 50 Gr.	0-95	14-8	16-8	1-60	10-5	22	+ KCl 64-0 Gr.	0-30	—	—	—	—

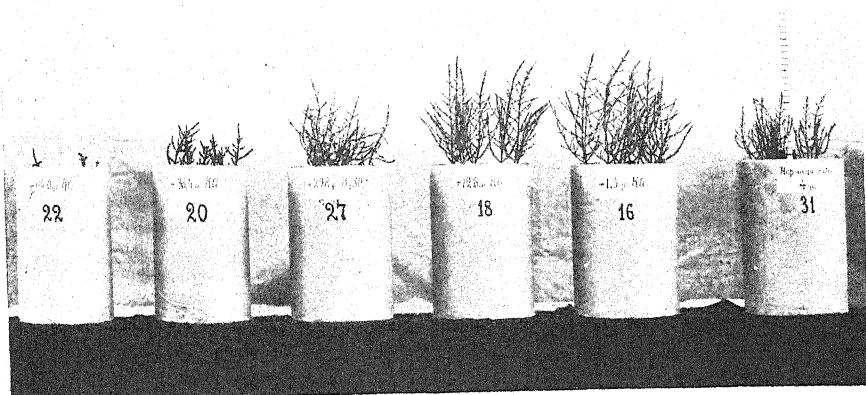


FIG. 2.

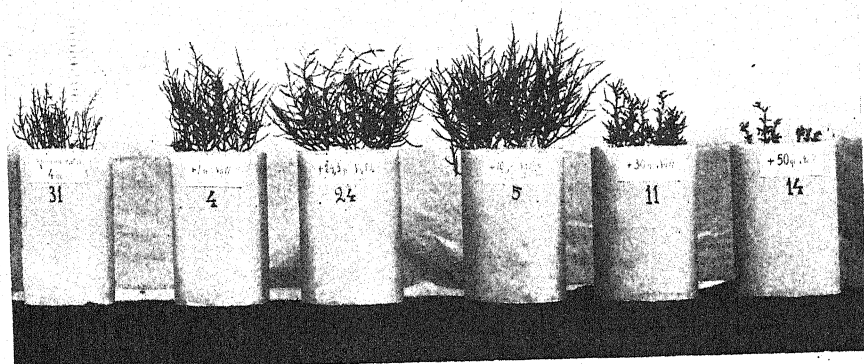


FIG. 3.

FIG. 2 und 3. *Salicornia herbacea* L., Sandkulturen.

Tabelle VI. Das Gewicht der Ernte in Sandkulturen auf ein Exemplar berechnet.

S.-n.	Gehalt an Salz im Gefäß, abgesehen von der normalen Nährstofflösung	Oberirdische Teile			Wurzeln	Gefäßnummern	Gehalt an Salz im Gefäß, abgesehen von der normalen Nährstofflösung	Oberirdische Teile			Wurzeln
		Gewicht im frischen Zustande in Gr.	Gewicht im absolut trockenem Zustande in Gr.	Wassergehalt %				Gewicht im frischen Zustande in Gr.	Gewicht im absolut trockenem Zustande in Gr.	Wassergehalt %	
1	nur Normal-lösung	1-12	0-1434	87-2	0-0278	—	—	—	—	—	—
4	+NaCl 1 Gr.	4-94	0-4594	90-7	0-0638	16	+KCl 1-3 Gr.	4-28	0-4066	90-5	0-1189
4	+Na <sub>2</sub> SO <sub>4</sub> 24-3 Gr.	8-89	0-7823	91-2	0-1275	27	+K <sub>2</sub> SO <sub>4</sub> 29-8 Gr.	2-30	0-2921	87-3	0-0379
5	+NaCl 10 Gr.	14-84	0-8162	94-5	0-1424	18	+KCl 12-8 Gr.	3-24	0-3349	91-5	0-2412
1	+NaCl 30 Gr.	4-51	0-3202	92-9	0-0233	20	+KCl 38-4 Gr.	1-42	0-1292	90-9	0-0228
4	+NaCl 50 Gr.	1-21	0-1065	91-2	0-0104	22	+KCl 64-0 Gr.	0-3	0-0543	81-9	0-0036



FIG. 4. *Salicornia herbacea* L., Sandkulturen.

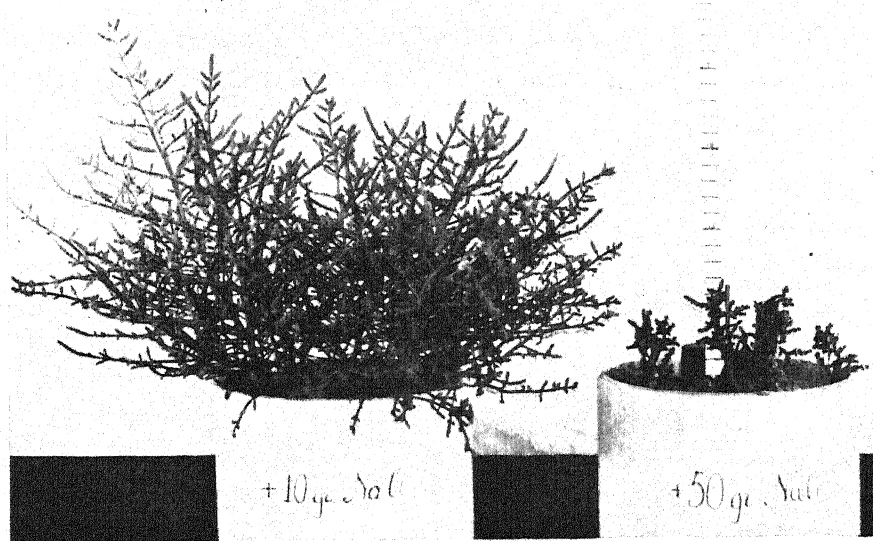


FIG. 5. *Salicornia herbacea* L., Sandkulturen.



Tabelle VII. *Ergebnisse der Plasmolyse und des Gehaltes an Salzen bei Exemplaren von Salicornia der Sandkulturen. (Das Zeichen ; scheidet die Zahlen, welche zu verschiedenen Exemplaren gehören.)*

Gefäß- num- mern	Der Salzge- halt im Ge- fäß, abgesehen von der nor- malen Nähr- stofflösung	Der Gehalt an NaCl in Gram. auf 100 Cub. Cent. der plasmolysie- renden Lö- sung bei dem Anfang der Plasmoly- se	Gehalt an Asche	Gehalt an NaCl (Cl er- mittelt und auf NaCl um- gerechnet)	Gefäß- num- mern	Der Salzgehalt im Gefäß, abgesehen von der nor- malen Nähr- stofflösung	Der Gehalt an NaCl in Gram. auf 100 Cub. Cent. der plasmolysie- renden Lö- sung bei dem An- fang der Plasmolyse	Gehalt an Asche	Gehalt an NaCl (Cl er- mittelt und auf NaCl um- gerechnet)
31	nur Nor- mallösung	3; 3	3	0.13	—	—	—	—	—
4	+ NaCl 1 Gr.	4; 4	2.4	1.03	16	+ KCl 1.3 Gr.	4; 4	2.9	1.7
24	+ Na <sub>2</sub> SO <sub>4</sub> 24.3 Gr.	4; 4	3.4	1.7 nicht NaCl, sondern Na <sub>2</sub> SO <sub>4</sub>	27	+ K <sub>2</sub> SO <sub>4</sub> 29.8 Gr.	4; 4	—	—
5	+ NaCl 10 Gr.	4; 4	2.7	1.4	18	+ KCl 12.8 Gr.	4; 4	3.6	2.8
11	+ NaCl 30 Gr.	5; 5	3.5	2.7	20	+ KCl 38.4 Gr.	6; 6	4.8	4.2
14	+ NaCl 50 Gr.	7; 8	5	4.3	22	+ KCl 64.0 Gr.	8	—	—

Zu den Tabellen V–VII. Die Versuche waren in Sandkulturen angestellt (Glasgefäße mit 5.5 Kil. Sand). Der Nährstoffzusatz bestand aus Ca(NO<sub>3</sub>)<sub>2</sub>—2 Gr., KNO<sub>3</sub>, KH<sub>2</sub>PO<sub>4</sub>, MgSO<sub>4</sub> + aqu., Fe<sub>3</sub>(PO<sub>4</sub>)<sub>2</sub> 8 aqu.—je 0.5 Gr.; in einige Gefäße waren Natron- und Kaliumsalze eingeführt in äquimolecularem Verhältnisse zu Chlornatrium; der Sand war mit Wasser vollständig gesättigt (1230 Gr. Wasser pro Gefäß). In jedem Gefäße waren 6 Exemplare gezogen, und alle Samen waren einem Exemplare entnommen; zu jedem Gefäße gehörte ein Kontrollgefäß.

### Die Versuchsergebnisse.

1. Das Glasschmalz verträgt nicht nur die Versalzung, sondern entwickelt sich bei einem mittleren Grade derselben am besten, zeigt einen starken Wuchs, ein ansehnliches Gewicht im frischen Zustande, und ein obgleich im minderen Grade vermehrtes Trockengewicht. Das Glasschmalz zeigt mit andern Worten eine ausgeprägte Osmophilie.

2. Das Glasschmalz, bei normaler Nährstofflösung gezogen, bleibt nicht nur im Wuchse und in der Gliederung des Pflanzenkörpers zurück, sondern hat auch sehr dünne assimilierende Glieder mit intensiverer grüner Färbung und eine grössere (pro Volumeinheit) Transpirationsfläche. Der Zusatz einiger Salze ruft bei dem Glasschmalze diejenigen Besonderheiten hervor, welche die aus natürlichen Standorten stammende Exemplare charakterisieren: eine stark ausgeprägte Sukkulenz, eine bleichere gelblich-grüne Färbung, eine kleinere Transpirationsfläche im Vergleich zu dem Volumen.

3. Wenn man den Einfluss der entsprechenden Salze im äquimolekularem Verhältnisse auf die unter 1 u. 2 erwähnten Merkmale des Glasschmalzes nach den Ergebnissen meiner Versuche vergleicht, so sieht man, dass die Natronsalze stärker als die Kalisalze, die Chloride stärker als die Sulfate wirken.

4. Eine besonders starke Wirkung wurde durch das Chlornatrium hervorgebracht; bei einem gewissem mittleren Gehalt von NaCl in den Sandgefässen (ungefähr 0·8 % auf Wasser nach dem Zugiessen des letzteren berechnet) und mit 1 % bei den Wasserkulturen erhielt man eine üppige Entwicklung des Glasschmalzes—viel stärker als bei den aus der Natur stammenden Exemplaren. Die Kurve der Entwicklung senkte sich zu beiden Seiten dieses Optimums (bei einer Verminderung oder Vergrösserung des Gehaltes an NaCl).

5. Das Merkmal der Sukkulenz zeigt einen anderen Kurvencharakter; die Kurve steigt an mit dem Steigen des Gehaltes von NaCl im Substrat.

6. Die Chloride von Na und K brachten schon selbst in kleinen Quanta, im Verhältnisse zu den andern Salzen der normalen Nährstofflösung, eine sehr bemerkliche Vermehrung der Sukkulenz und eine Verstärkung der Entwicklung bei dem Glasschmalz hervor (ein jedes Gefäss enthielt 4 Gr. Nährstoffgemisch und die starke Wirkung war durch einen Zusatz von 1 Gr. NaCl oder des äquimolekularen Quantum von 1·3 Gr. KCl erreicht). Die Wirkung der beiden Salze in den angegebenen kleinen Quanta war eine fast gleiche.

7. Bei einem höheren Gehalt an Chlorkalium war die Wirkung dieses Salzes auf das Glasschmalz eine andere als diejenige des Chlornatrium. Bei einem höheren Zusatz von KCl (12·8 Gr. pro Gefäss) war keine stärkere Entwicklung, wie es bei einem erhöhten Zusatz von Chlornatrium der Fall war, bemerkt worden; die Pflanze entwickelte sich sogar etwas, wenn auch nicht viel, schwächer. Auch waren der Wuchs und die Entwicklung des Glasschmalzes bei einem hohen Gehalt an KCl weit schwächer, als bei denjenigen Kulturen, die mit einem äquimolekularen Quantum von Chlornatrium gezogen waren. Da, wo der Zusatz von Chlorkalium am grössten war (64 Gr. pro Gefäss), wurde ein teilweises Absterben der Exemplare bemerkt. Die Kurve der Entwicklung des Glasschmalzes für die erprobten Zusätze von Chlorkalium hat ihren höchsten Punkt gleich am Anfange; und man kann wohl vermuten, dass bei der höchsten Konzentration, welche angewendet war, das Chlorkalium auf das Glasschmalz giftig einwirkte.

8. Das Natriumsulfat kann bei dem Glasschmalz eine starke Entwicklung, grosse Sukkulenz und einen hohen Wuchs hervorbringen. Seine Wirkung aber stand derjenigen des Chlornatrium im äquimolekularem Quantum bemerklich nach. Es kann wahrscheinlich als eine Regel betrachtet werden, dass  $\text{Na}_2\text{SO}_4$  im Vergleich mit NaCl in gegebener Hinsicht schwächer wirkt.

9. Eine verhältnismässig schwache antreibende Wirkung auf den Wuchs und die Sukkulenz wurde durch Kaliumsulfat (im äquimolekularen Quantum mit  $\text{Na}_2\text{SO}_4$  und demjenigen Zusatz von NaCl, welcher ein üppiges Wachs-

tum des Glasschmalzes hervorbrachte) erreicht. Der grosse Gehalt an Kaliumsalz im Substrat übte wahrscheinlich eine vergiftende Wirkung auf die Pflanze aus.

10. Erinnern wir uns noch, dass nach den Versuchen von Batalin eine Lösung von Magnesiumsulfat, welche bei einer allmählich wachsenden Konzentration zum Begiessen gebraucht wurde, bei dem Glasschmalz keine bemerkbare Sukkulenz im Vergleich mit Pflanzen, die einer Versalzung nicht unterworfen waren, hervorbrachte.

11. Demnach kann man sich nur mit einigen Einschränkungen, den auf Beobachtungen des natürlichen Zustandes gestützten Ausführungen von T. Bernatsky anschliessen, dass die Qualität der Salze wenig Einfluss auf die Vegetation der Salzböden hat. Dennoch kann nicht nur Natriumchlorid, oder Natriumsulfat, sondern, wie es sich denken lässt, auch Kaliumchlorid in natürlichen Bedingungen, Salzböden bilden mit charakteristischen Associationen der typisch entwickelten *Salicornia herbacea* L.

12. Ermittlungen durch Plasmolyse zeigen, dass die Exemplare des Glasschmalzes bei üppigem Wuchs, unter der Wirkung geeigneter Salze, den osmotischen Druck nur wenig erhöhen; oder auch wohl denselben Druck aufweisen, wie die Pflanzen, die bei einem normalen Nährstoffgemisch gezogen sind. Nur bei einer starken Unterdrückung des Wuchses durch Versalzung wird der osmotische Druck bedeutend wachsen. Es scheint als ob bei dieser Pflanze ein Korrelationsverhältniss zwischen dem Wuchs und dem osmotischen Druck besteht. Die Verstärkung des osmotischen Druckes bis zu einem gewissen Grade, dient als innerer Faktor, welcher einen verstärkten Wuchs hervorbringt, anderseits wenn das Wachsen mit einer gewissen Intensität vor sich geht, kann die Druckvergrösserung nicht zu hoch ansteigen.

13. Bemerken wir noch, dass nach unseren Versuchen die Verstärkung des Wuchses, die Vergrösserung der Sukkulenz und die Erhöhung des osmotischen Druckes unter dem Einfluss von Chlornatrium bei dem Glasschmalz auch bei fast unterdrückter Transpiration in den vergleichenden Kulturen unter Glas in feuchten Kammern vor sich geht.

14. Wir besprechen nicht die sehr interessante innere anatomische Veränderungen, die bei dem Glasschmalz unter dem Einfluss der Versalzung stattfinden. Viele dieser Veränderungen sind schon in der Literatur teilweise angegeben (Batalin, Lesage u. a.). Wir erwähnen nur die interessante Erscheinung, dass die Zellen, welche wegen der Versalzung grössere Dimensionen annehmen, auch grössere Zellkerne aufweisen.

### 3. ZUR GESCHICHTE DER VEGETATION DES GLASSCHMALZES IN SEINEN NATÜRLICHEN STANDORTEN.

Die Ansicht Schimpers, dass eine Aehnlichkeit in Form und Bau zwischen den Halophyten und den Xerophyten in manchen wesentlichen Zügen besteht, und die Erklärung, welche Schimper dieser Erscheinung gab, wurde öfters

bestritten. Wir werden nur folgende wichtigen Bemerkungen von Fitting anführen.

“Schimper meint, und nach ihm viele andere oekologische Pflanzengeographen, dass nämlich die Salzanhäufung eine notwendige Folge der Transpiration sei, so dass mit der Vergrößerung der Transpiration auch die Salzkonzentration des Zellsaftes steigen müsse. Meine Beobachtungen zeigen indessen, dass die Salzaufspeicherung und ihr Grad auf spezifischen Befähigungen der Pflanzen beruhen, aber von der Transpirationsintensität ganz unabhängig sind. Ueber die Aufnahme des Kochsalzes entscheiden eben die Permeabilitätsverhältnisse der Plasmahäute, über seine Anhäufung und Speicherung—entsprechende Befähigungen der Pflanze, aber nicht die Transpiration; anders wird die Salzarmut lebhaft transpirierender Pflanzen von trockenen Wüstenstandorten und mancher Pflanzen aus den Salzstümpfen nicht verständlich.”

“Auch die auf Schimper zurückgehende Lehrmeinung, dass der xerophyte Bau der Pflanzen, deren Standort wasserreich ist, dadurch erklärt werden kann, dass die salzhaltigen Böden physikalisch als trocken anzusehen sind, erregt manches Bedenken, zum wenigsten bis diese Ansicht durch exakte aus Versuchen stammende Angaben bestätigt ist: von rein physikalischen Gesichtspunkten scheinen alle Schwierigkeiten der Wasserversorgung in einem salzhaltigen Boden überwunden, wenn die darin wachsenden Pflanzen durch Erhöhung der Zellsaftkonzentration ein entsprechendes Konzentrationsgefälle, wie im salzfreien Boden unterhalten.”

Die Arbeiten Fittings weisen den Mangel auf, dass der genannte Forscher durch geeignete Bodenanalyse den Gehalt der leicht löslichen Salze in verschiedenen Bodenschichten nicht ermittelt hat und auch nicht die Zuordnung der Wurzelsysteme zu diesen Schichten erkannt hat. In der “Hungerwüste” in Turkestan habe ich am selben Standort das Kameelgras (*Alhagi camelorum* Fisch.) und sukkulente Salzpflanzen (wie *Halocharis hispida* C. A. Mey., *Salsola crassa* M. B., *Salsola lanata* Pall. und sogar den Glasschmalz (*Salicornia herbacea* L.) angetroffen. Das Kameelgras, trotz seiner unzweifelhaft hohen Transpirationsintensität wird nur eine geringe Menge leicht löslicher Salze anhäufen, während der Gehalt an diesen Salzen bei den fleischigen Salzpflanzen ganz enorm anwächst. Es wäre aber ein grosser Fehler, wenn wir annehmen würden, dass die genannten Pflanzen unter denselben Bedingungen der Versalzung leben, und nur in Folge ihrer spezifischen Eigentümlichkeiten die Salze in solchen verschiedenen Graden anhäufen. Das Kameelgras senkt seine saugenden Wurzeln in die tiefen an Süsswasser reichen Schichten des Substrats, während die sukkulenten Salzpflanzen in der obersten, sehr salzreichen Bodenschicht wurzeln.

Es ist nicht möglich der kategorischen Aussage von Fitting, dass die Aufspeicherung der Salze, und deren Grad von der Transpirationsintensität unabhängig ist, beizutreten; man müsste demnach die Transpiration ganz

unabhängig von den übrigen Lebenserscheinungen der Pflanzen und von den natürlichen Mitbedingungen betrachten.

Die Widerlegung der Ansichten von Schimper durch Fitting verliert demnach ihre Kraft; anderseits müssen die Ansichten des erstgenannten Forschers nur als eine vorläufige enge Formel für die Auslegung einiger ins Auge fallenden Besonderheiten der Halophyten angesehen werden—eine Formel von unbedeutendem Inhalt.

Wenn wir den Naturerscheinungen näher rücken, so finden wir, dass dieselben viel tiefer und viel inhaltsreicher als das zur Orientierung angelegte Schema sind. Die Pflanze muss sich nicht nur gegen die Wirkung der Aussenwelt schützen, sondern sie muss noch die Befähigung haben die verschiedenen Eigenschaften und Kräfte derselben gehörig auszunützen um ihre natürlichen Lebenserscheinungen sicher zu stellen.

Wenn wir uns von diesen allgemeinen Betrachtungen wieder dem Glasschmalz zuwenden, so wollen wir versuchen ein ungefähres Schema der vegetativen Entwicklung dieser Pflanze auf salzhaltigem Boden aufzubauen.

Das Glasschmalz ist ein wasserliebendes Halophyt, und in der ersten Zeit der Keimung fast eine Wasserpflanze. Die Verbreitung seiner Früchte soll durch die Mitwirkung von Wasser erfolgen; dort wo die Früchte bei dem Zurückziehen des Wassers auf dem Meer—oder Seestrände liegen bleiben, dort bemerkt man charakteristische Reihen der Exemplare von Glasschmalz, die parallel der Uferlinie gehen. Das Keimen der betrachteten Pflanze erfolgt in Salzböden in einem nassen Grunde, oder sogar im Wasser, bei einer verhältnissmässig schwachen Konzentration leichtlöslicher Salze. Versuche haben gezeigt, dass die *Salicornia herbacea* im destillierten Wasser vortrefflich keimt, aber für Salzreichtum ein grosse Anpassungsfähigkeit besitzt, da sie noch in einer 2 % Lösung von NaCl ziemlich gut keimt.

Nach dem Keimen scheint es, als ob das Glasschmalz durch die Versalzung in seinem Wuchse angetrieben wird, und so die Möglichkeit bekommt für sein vegetatives Leben die günstigere Frühlingsperiode auszunützen; zu dieser Zeit sind nämlich die Salzböden wasserreicher, die Konzentration der Salzlösungen hat noch nicht ihren höchsten Grad erreicht, auch ist die Sonnenhitze weniger fühlbar. Wir sehen auch in den entsprechenden Kulturen, dass bei einer gewissen mittleren Salzhaltigkeit, welche doch im absoluten Betrage als eine recht bedeutende gelten mag, erhält die *Salicornia* einen mächtigen Impuls zu ihrer Entwicklung, wächst und verzweigt sich stark. Eine gewisse Zeit nach dem Keimen wächst das Glasschmalz ziemlich langsam, indem hauptsächlich nur die Kotyledonen sich vergrössern, während auch leichtlösliche Salze in der Pflanze aufgespeichert werden.

In dieser Vegetationsphase bleibt der osmotische Druck in den Zellen der Pflanze selbst auf salzreichem Substrat verhältnissmässig gering und die Befähigung die Transpirationsintensität zu beschränken bleibt viel schwächer. Es darf aber nicht vergessen werden, dass der austrocknende Einfluss der

Aussenwelt auf die assimilierenden Sprossen des Glasschmalzes viel schwächer ist; anderseits ist es vielleicht der Pflanze günstig in dieser Periode eine höhere Transpirationsintensität einzuhalten, um während des verstärkten Wachstums bei geringerer Versalzung im Substrat demselben den Nährstoff schneller zu entziehen.

Die Erhöhung des osmotischen Druckes während dieser Entwicklungsphase wird durch das Wachsen verlangsamt: das Anhäufen der Salze geht weiter, aber die Salze verteilen sich in einer grösseren inneren Masse. So kommen wir dem Gedanken Schimpers etwas näher, da letzterer sich ausspricht, dass das wassertragende Gewebe der Halophyten "zum Schutze der assimilierenden Zellen gegen eine schädliche Konzentration der Salze eingerichtet ist und wird demgemäss mit dem Altern der Blätter und der Vermehrung ihres absoluten Gehaltes an Salz wohl überflüssig."

Bei Antritt einer wärmeren und trockeneren Sommerzeit vergrössert sich die Konzentration der Salze im Substrat, welches die Wurzeln unserer Pflanze umgibt. Bald steigt sie höher als das Optimum für die betrachtete Salzpflanze. Das Anwachsen wird verlangsamt, und eine bedeutende Aufspeicherung der Salze tritt im Inneren des Pflanzenkörpers ein, wobei der osmotische Druck im Zellsaft zu einer enormen Höhe anwächst. Zugleich erhält die Pflanze eine grosse Widerstandsfähigkeit in ihren assimilierenden Sprossen gegen die Sonnenhitze und die austrocknende Wirkung der Atmosphäre: die Befähigung für intensive Transpiration wird bedeutend schwächer, obgleich die Transpiration dennoch mit genügender Intensität erfolgt und einen regelmässigen Tagesgang aufweist.

Das Glasschmalz absorbiert während dieser Phase seiner vollen vegetativen Entwicklung absolut nur wenig Wasser, gibt aber letzteres zweckmässig für die Unterhaltung einer ziemlich intensiven Transpiration aus. So hält es seine Spaltöffnungen für die Absorption von  $\text{CO}_2$  offen. Ausserdem ist es wahrscheinlich, dass eine gewisse Transpirationsintensität auch deshalb unterhalten werden muss, um die assimilierenden Sprossen während der Sommerperiode gegen eine übermässige Erwärmung durch die Sonne zu schützen.

Die charakteristische Befähigung mit einem kleinen Quantum Wasser eine mehr oder minder hohe Intensität der Transpiration zu unterhalten kann mit den folgenden Charakterzügen der Organisation des Glasschmalzes in Verbindung gebracht werden: (1) die Oberfläche der Pflanze pro Volumeinheit ist nicht gross; (2) die assimilierenden Organe in den niedrig-wachsenden Büschchen der Pflanze erheben sich nur wenig über den Boden; die Transpirationsfläche liegt nahe an den wichtigeren wasserleitenden Gefässen und nahe an den Wurzeln, die dasselbe ansaugen.

Das Glasschmalz kann noch mit Wassermangel kämpfen und sich auch vom Ueberflusse der Salze befreien, indem es einen Teil seiner Blätter abwirft: die grüne, saftige Rinde an seinen Gliedern wird gelb, verliert das Chlorophyll, fällt nachher ab, und vertrocknet. Dieser Process beginnt am unteren Teile

des Büschelchens und setzt sich allmählich an dem Hauptspross und den Zweigen fort<sup>1</sup>.

Ein solches Abwerfen der Blätter zieht sich langsam während des Alterns des Glasschmalzes fort, besonders aber dann, wenn die Pflanze zum Blühen und Fruchttragen übergeht.

Das angedeutete Vergleich-Schema findet seinen Ausdruck in der Tabelle VIII.

Tabelle VIII. Die Phasen der vegetativen Entwicklung des Glasschmalzes in Verbindung mit den Veränderungen der äusseren Bedingungen.

	Die Feuchtigkeit des Substrates	Der Salzgehalt des Substrates	Die austrocknende Wirkung des oberirdischen Mediums auf die assimilierenden Sprossen	Die Phasen der vegetativen Entwicklung des Glasschmalzes	Die Befähigung für intensive Transpiration	Die Resistenz der assimilierenden Sprossen gegen die austrocknende Wirkung des Mediums	Die Aufspeicherung leicht löslicher Salze im Pflanzkörper
Frühling	eine sehr reichliche; öfters Ueberschwemmen mit Wasser	vergleichsweise gering	schwach	(a) das Keimen		gering	
				(b) ein starkes Wachsen in die Länge	hoch	noch ziemlich schwach	geht langsam vor und erreicht kein hohen Grade
Sommer	nach und nach vermindert; Boden bleibt jedoch immer feucht	sehr gross	stark (grosse Sonnenhitze)	(c) das Wachsen verlangsamt sich und hört auf	fällt bis zu einem niedrigen Grade	steigt bis zu einer sehr bedeutenden Grösse an	

Man kann das Schema als einen Masstab für die Bewertung der Entwicklung des Glasschmalzes in verschiedenen Variationen dieser Entwicklung in den natürlichen Standorten der Pflanze benützen. Als Illustration werden zwei Beispiele angeführt.

In der Umgebung von Sarepta unweit der Ansiedlung "Teplje Wody" auf einem Salzboden mit *Salicornia herbacea* bewachsen, hatten die Exemplare dieser Pflanze am 21 Juli 1913 eine mittlere Höhe von 5–8 Cent. und als Grenzhöhe 15 Cent. erreicht. Das Glasschmalz war schon in Blüte. Am 16 August 1912 auf demselben Salzboden waren als mittlere Höhe 6–12 Cent. und als Grenzhöhe—18 Cent. beobachtet.

Ein anderes Bild wurde am 15 August 1916 auf einem salzhaltigen Feldstücke einer künstlich bewässerten Baumwollenplantage der "Hungersteppe" in Turkestan beobachtet. Das Glasschmalz war hier als Unkraut verbreitet und zeigte eine ausnahmsweise reiche Entwicklung. Die Exemplare dieser Pflanze hatten eine mittlere Höhe von 15–35 Cent., und eine Grenzhöhe von

<sup>1</sup> Wir stimmen völlig mit den vor längerer Zeit ausgesprochenen Ansichten von Duval-Jouve überein, dass die sukkulenten assimilierenden Glieder der *Salicornia herbacea* einen zusammengesetzten Bau aufweisen; sie bestehen nämlich aus Stengeln mit angewachsenen umschliessenden Blättern. Zu Gunsten dieser Ansicht sprechen auch die bei unseren Kulturen vorgefundenen interessanten Anomalien.

42 Cent. Die schönsten Exemplare hatten die folgenden Dimensionen in Centimeter.

Höhe ... ..	32	34	38	33	37
Der Durchmesser in zwei zu einander rechtwinklig stehenden Richtungen ...	28-31	34-42	42-43	41-47	38-47

Eine von diesen Pflanzen hatte ein Gewicht von 338.5 Gr. Es muss noch erinnert werden, dass die unter der Wirkung von NaCl am üppigsten entwickelten Exemplare unserer Kulturen nur eine Höhe von 17.2-22.9 Cent. und ein Mittelgewicht von 14.84 Gr. besaßen. Das Glasschmalz am angezeigten Standorte in der "Hungersteppe" war so zu sagen "zu Gras gewachsen" und war an der Zeit noch nicht zu Blüte gekommen.

Bei einer Zusammenstellung der Angaben über den Wuchs des Glasschmalzes mit den Data über Feuchtigkeit, Versalzung und osmotischen Druck zeigen sich folgende Ergebnisse:

- (a) in der Umgebung von Sarepta ist die Versalzung stark, der Wuchs dagegen niedrig und der osmotische Druck sehr gross;
- (b) auf der Baumwollenplantage in der "Hungersteppe" ist die Versalzung weit geringer, der Wuchs aber ausserordentlich stark, der osmotische Druck dagegen viel kleiner.

In Anlehnung an unser Schema werden wir die folgende Erklärung der angedeuteten Verschiedenheiten geben. Auf den Salzböden bei Sarepta steigt die Konzentration der Salze rasch, und ist vom Anfange an vielleicht höher als das Optimum für die betrachtete Pflanze. In der "Hungersteppe" haben wir einen Boden mit schwächerer Versalzung künstlich bewässert; alles dies wirkte günstig während der Phase des starken Wachstums.

Die Sukkulenz bei dem Glasschmalz ist eine der charakteristischen Merkmale des Halomorphismus. Schon die alten Beobachtungen und Versuche von Lesage zeigen wohl an, dass auch bei den gewöhnlichen Pflanzen und nicht nur bei den Salzpflanzen die Wirkung von Chlornatrium eine gewisse Sukkulenz und eine Vergrösserung der Zellen hervorruft. Es ist deshalb möglich, dass dieses Merkmal sich bei dem unmittelbaren Einfluss der Aussenwelt und namentlich der Versalzung verstärkt.

Dasselbe Merkmal wird auch zum zweiten Male für das Gedeihen der Pflanzen auf versalzten Standorten nutzbar, und wurde auf denselben durch Selektion verstärkt. Ich verbleibe auf dem Standpunkte, dass wenn ein gegebenes Merkmal als Modifikation durch den Einfluss äusserer Bedingungen einer einseitigen konstanten und ununterbrochener Ablenkung unterworfen wird, so kann im Wege der Mutation eine vererbte Veränderung in demselben Sinne entstehen; das entsprechende "Gen" kann sich zu zweien, von eindeutigem Charakter, zergliedern, wenn die Ablenkung auf die Verstärkung des Merkmals einwirkt, oder in einen passiven Zustand übergehen, sich atrophieren, wenn das Merkmal geschwächt oder unterdrückt wird.

Aber bei einer für das Gedeihen auf Salzböden scharf specialisierten Form,



wie das Glasschmalz, bleibt doch eine in dieser Hinsicht sehr hohe Plastizität vorhanden. Es ist aber auch möglich, dass nur eine grosse Flexibilität, eine Befähigung die Sukkulenz unter dem Einfluss der Versalzung zu verstärken, und auch ein scharfer Effekt bei verhältnissmässig niedriger Konzentration einiger Salze, z. B. des NaCl und des KCl, bei dem Glasschmalze erblich fixiert ist.

Am Ende dieser Auslegung muss ich noch Folgendes bemerken. Wenn die Samen des Glasschmalzes in der Natur auf einen sehr feuchten, aber nicht versalzten Standort treffen, so wird die Pflanze gering wachsen, keine grosse Sukkulenz hervorbringen, gegen das Austrocknen schlecht geschützt und von andern Pflanzen unterdrückt sein. Im letzten Falle gilt wohl auch der Umstand, dass das Glasschmalz zu den lichtliebenden Pflanzen gehört, was mit der verhältnissmässig grossen Reduktion der lichtempfangenden Oberfläche im Zusammenhange steht.

## II. UNTERSUCHUNGEN ÜBER DAS HALOPHYT— *FRANKENIA PULVERULENTA* L.

Die *Frankenia pulverulenta* L.—eine einjährige Miniaturpflanze—wurde zum monographischen Studium als ein echter Vertreter des zweiten oben ange-deuteten Typus der Halophyten, d. h. der nicht sukkulenten Pflanzen, welche die leichtlöslichen Salze in grosser Menge ausscheiden, erwählt.

Die Halophyten des betrachteten Typus haben im russischen Süd-Osten eine ansehnliche Menge von Vertretern. Solche sind z. B. die Species der *Frankenia* (*pulverulenta* L., *hirsuta* L.), die schönen Büsche der Tamarisken (z. B. *Tamarix Pallasii* Desv., *hispida* Willd.), die Species der *Statice* (*caspia* Willd., *tomentella* Boiss., *otolepis* Schrenk., *perfoliata* Karel. u.s.w.), *Cressa cretica* L., *Aeluropus littoralis* Parl. u. *repens* Parl. Die Pflanzen dieses Typus sind an solchen Standorten heimisch, wo eine grosse Salzhaltigkeit mit einer guten Wasserversorgung zusammentrifft. Sie spielen in dem Kreislauf der Salze in der Natur wohl eine bedeutende Rolle, und wirken gewissermassen wie Pumpen, welche die leichtlöslichen Salze aus den tieferen Schichten des Bodens auf die Oberfläche herauf ziehen.

Der Oekologie der Halophyten vom betrachteten Typus ist eine wichtige, inhaltsreiche Arbeit Ruhlands gewidmet, welcher sich hauptsächlich mit der Untersuchung über die *Statice Gmelini* Willd. befasste.

Ausser anderen wertvollen Ergebnissen hat Ruhland auch eine gute experimentelle Begründung für eine Ansicht über die physiologische Bedeutung der Salzausscheidung bei den betreffenden Halophyten, welche schon längst von mehreren Autoren (auch von mir) ausgesprochen war, gegeben.

Nach dieser Ansicht hat die reichliche Ausscheidung der leichtlöslichen Salze den Zweck, der Pflanze für die Befreiung der lebenden Zellen vom Ueberfluss solcher Salze behilflich zu sein.

Nachfolgend bringen wir in einer sehr gedrängten Form einige Angaben über unsere Versuche, insofern sie die Angaben Ruhlands ergänzen.

1. Es ist durch unsere Versuche erwiesen, dass die Entwicklung der *Frankenia pulverulenta* durch Versalzung nicht verstärkt wird, wie es bei der *Salicornia herbacea* der Fall ist. In den Kulturen, welche eine Normalsalzmischung enthalten, so wie auch in denjenigen mit einem Zusatz von 0.1 %, 0.5 % und 1 % Kochsalz, entwickelt sich die *Frankenia pulverulenta* sehr üppig, und in fast derselben Weise, wie bei der Normalmischung; bei stärkerer Salzhaltigkeit (3 u. 5 % NaCl) wurde schon eine bedeutende Unterdrückung des Wachstums beobachtet. Andererseits, in stark salzhaltigen Kulturen welkten die Pflanzen nicht so leicht, die Blätter blieben frisch, und der osmotische Druck in den Blättern wurde merklich erhöht.

2. Die Tröpfchen auf den Pflanzen stammen hauptsächlich oder fast ausschliesslich (bei den normalen Kulturen) von dem Wasser, das von dem Innern der Pflanzen ausgeschieden wird. Die Kondensation des Wassers aus der Atmosphäre während einer ganzen Nacht in der feuchten Kammer ist unbedeutend, gewinnt aber an Bedeutung, je nach der Verstärkung der Salzhaltigkeit.

Als eine Erläuterung mag die folgende Tabelle dienen (nach den Versuchen mit Sandkulturen—3 Exemplare der *Frankenia* in einem jeden Gefäss).

Tabelle IX. Gewichtsgewinn—bez. Verlust an Tröpfchen in Gramm.

23. viii.

Gefässnummer und Salzhaltigkeit	Während der Nacht in der feuchten Kammer 7½ Uhr Ab.—5½ Mor.	Gewichtsverlust nach Abwischen mit Löschpapier	Prozente zur täglichen Verdunstung am 21 August (5½ Uhr Mor. — 6½ Ab.)	
			Wasser aus der Atmosphäre kondensiert	Lösung von der Pflanze ausgeschieden
1 nur Normalmischung	0.0 Ziemlich viele kleine Tröpfchen	1.9	0.0	2.1
3 Normalsch. + 1 % NaCl	+ 1.1 Zahlreiche Tröpfchen	—	—	—
2 Normalsch. + 2 % NaCl	+ 2.1 Zahlreiche Tröpfchen	—	—	—
4 Normalsch. + 3 % NaCl	+ 3.1 Sehr zahlreiche Tröpfchen	9.5	5.5	7.3

Es lässt sich aus der Tabelle ersehen, dass bei den nicht versalzten Kulturen das Quantum des an der Pflanze angesammelten flüssigen Wassers, im Vergleich zu der täglichen Ausscheidung sehr unbedeutend ist, in den versalzten Kulturen aber ist dieselbe viel stärker.

3. Wie man es aus derselben Tabelle teilweise ersehen mag, ist die Ausscheidung der Flüssigkeit aus dem Innern der Pflanze, bei den versalzten Kulturen weit grösser, als bei den nicht versalzten, wenigstens so lange bis die Versalzung keinen all zu hohen Grad erreicht. Diese Ergebnisse wurden durch Versuche sowohl mit vollständigen Pflanzen, als auch mit abgeschnittenen Trieben vielfach bestätigt. Wir führen hier noch zwei Tabellen an. (Siehe auch Fig. 6 u. 7.)



FIG. 6. *Frankenia pulverulenta* L. Früh Morgen. Flüssigkeit- und Salzausscheidungen bei den nicht versalzten und versalzten Kulturen. Ziffern bezeichnen Centimeter.



FIG. 7. *Frankenia pulverulenta* L. Am Tage Salzausscheidungen bei den nicht versalzten und versalzten Kulturen. Ziffern bezeichnen Centimeter.

Tabelle X. Die Ausscheidung des Wassers in der feuchten Kammer, durch die abgeschnittenen Pflanzentriebe, bei den Pflanzen welche ohne Versalzung kultiviert wurden.

8. ix. 5½ Uhr Ab.—9. ix. 11 Uhr Morg.

	Die Flüssigkeit im Gefäss	Gewicht der Triebe bei Anfang des Versuchs in Gr.	Veränderung des Gewichtes zum Ende des Versuchs in Gr.	Der Gewichtsverlust in der feuchten Kammer pro 1 Gr.	Flüssigkeit ausgeschieden pro 1 Gr. des ursprünglichen Gewichtes der Triebe
1	Wasser	0.951	+ 0.209	0.074	0.70
2		0.682	+ 0.126	0.079	0.85
Summe		1.633	+ 0.335	0.076	0.77
5	NaCl 3 %	0.852	+ 0.096	0.063	1.20
6		0.830	+ 0.092	0.050	1.20
Summe		1.682	+ 0.188	0.056	1.20
7	NaCl 7 %	1.103	− 0.063*	+ 0.022	0.69
8		0.893	− 0.083*	0.000	0.61
Summe		1.996	− 0.146	+ 0.011	0.65

\* Merkliehe Schlawheit und Senkung der Zweige.

Tabelle XI. Ausscheidung der Flüssigkeit in der feuchten Kammer, durch die abgeschnittenen Triebe von Pflanzen ohne Versalzung gezogen (in Grammen).

9. ix. Fn. Mit.—10. ix. 11 v. Mit.

	Die Flüssigkeit im Gefäss	Gewicht des Triebes am Anfang des Versuchs	Gewichtsveränderung zum Ende des Versuchs	Gewichtsverlust in der feuchten Kammer pro 1 Gr.	Flüssigkeit ausgeschieden pro 1 Gr. des ursprünglichen Gewichtes der Triebe	Gewichtsverlust des Triebes durch Verdunstung und die Wassertröpfchen + Gewichtsvermehrung des Triebes	Gewichtsverlust der Flüssigkeit im Gefäss
1	Wasser	1.129	+ 0.241	0.060	0.73	0.887 + 0.241 = 1.128	1.170
2		0.662	+ 0.143	0.041	0.60	0.424 + 0.143 = 0.567	0.599
Summe		1.791	+ 0.384	0.050	0.66	1.695	1.769
3	NaCl 1 %	1.093	+ 0.165	0.044	0.95	1.090 + 0.165 = 1.255	1.270
4		0.759	+ 0.123	0.053	1.07	0.853 + 0.123 = 0.976	1.027
Summe		1.852	+ 0.288	0.048	1.01	2.231	2.297

4. Die äusseren Ausscheidungen leichtlöslicher Salze sind als eine äussere osmotische Verrichtung anzusehen, welche das Wasser aus dem Innern der Pflanze ansaugt. In dieser Hinsicht differieren unsere Angaben von den Ergebnissen Ruhlands. Unsere Aussagen sind hingegen durch zahlreiche Versuche, die in mannigfacher Weise variirt waren, bekräftigt worden. So haben wir gefunden, dass nach dem Abwischen mit Löschpapier, die Befähigung der Pflanzen von versalzten Kulturen das Wasser in ausgiebiger Weise aus dem Innern der Pflanze auszuschcheiden sich bemerklich verminderte. Diese Befähigung wird aber wieder im grösseren Masse hergestellt, wenn man die Pflanze mit einer Lösung von Kochsalz bespritzt und die neuerschiedenen Tröpfchen austrocknen lässt, wobei ein Salzanflug an der Oberfläche verbleibt. (Siehe Tabelle XII.)

Tabelle XII. Einfluss der Verwischung des Salzanfluges und des Bespritzens mit einer Lösung von NaCl auf die Ausscheidung der Flüssigkeit in Grammen.

(a)—während einer Nacht in der feuchten Kammer (6½ nach Mit.—5½ vor Mit.);  
 (b)—nach dem Abwischen mit Löschpapier um 5½ vor Mit.

Gefäßnummern	27. viii.		28. viii.		30. viii.		1. ix.	
	(a)	(b)	(a)	(b)	(a)	(b)	(a)	(b)
5 Normal + 3 % NaCl	+1.9	-5.2	-0.3	-1.7	-1.1	-2.2*	+4.5	-9.1
6 Normal + 3 % NaCl Kontrollgefäß	+1.3	—	+1.3	—	+1.2	—	+1.9	—

\* Die Pflanze wurde nachher mit einer 10 % Lösung von NaCl bespritzt, die während des Tages verdunstete.

Zu Tabelle XII. Ein ausserordentlich grosses Ausscheiden der Flüssigkeit aus dem Innern der Pflanze bei den unversalzten Kulturen, kann auch durch Bespritzen und nachfolgendes Austrocknen der Tröpfchen der Kochsalzlösung verursacht werden. Dasselbe Resultat kann auch endlich dann erreicht werden, wenn man die abgeschnittenen Triebe der *Frankenia pulverulenta*, von solchen Pflanzen stammend, die keiner Versalzung unterworfen waren und deren abgeschnittene Enden in destilliertes Wasser tauchen, mit gepulverten NaCl bestreut.

Tabelle XIII. Der Einfluss des Bestreuens der Triebe mit Kochsalz auf das Ausscheiden der Flüssigkeit. (Die Triebe waren von einer Pflanze abgeschnitten, die ohne Versalzung erzogen worden war.) In Grammen.

		Gewicht des Triebes bei dem Anfange des Versuchs	NaCl aufgestreut	Gewicht des Triebes am Ende des Versuchs	Gewichtsverlust in der feuchten Kammer	Gewichtsverlust nach dem Abwischen	Flüssigkeit auf ein Gramm des anfänglichen Gewichtes ausgeschieden	Gewichtsverlust des Triebes durch Verdunstung und Ausscheidung von Tröpfchen + Gewichtsvergrößerung des Triebes	Verminderung der Flüssigkeit im Gefäß
1	Wasser	0.512	—	+0.102	0.027	0.441	0.86	0.027+0.441+0.102=0.570	0.595
2		0.900	—	+0.149	0.037	0.790	0.88	0.037+0.790+0.103=0.976	1.038
Summe		1.412	—	+0.251	0.064	1.231	0.87	1.546	1.633
3		0.692	0.031	+0.103	+0.025	1.174	1.6	1.174-0.031-0.025+0.103=1.221	1.237
4		0.676	0.066	+0.085	+0.150	1.235	1.5	1.235-0.15-0.66+0.085=1.104	1.180
Summe		1.368	0.097	+0.188	+0.175	2.409	1.55	2.325	2.417

Platzmangel verhindert uns ein einheitlichere Bild des Lebens der *Frankenia pulverulenta* in deren natürlichen Bedingungen, wie wir es für das Glasschmalz gemacht haben, zu geben, und unsere Versuche mit dieser Pflanze zu beschreiben (man vergleiche unsere Arbeit in russischer Sprache, die eben druckfertig ist).

### III. DIE PFLANZE ALS LEBENDE MASCHINE.

Die Oekologie beschäftigt sich viel mit der Resistenzfähigkeit der Pflanzen gegen die Dürre. In den Lehrbüchern werden viele Eigenschaften angeführt, mit deren Hilfe die Pflanzen der trockenen Standorte, die Xerophyten, die

Wasserverdunstung einschränken und sich dadurch gegen die Vertrocknung schützen. In letzter Zeit ist diese Frage einer kritischen Umarbeitung unterworfen worden. Es wurde hervorgehoben, dass viele Pflanzen (mit den Merkmalen der Xerophyten) leicht und schnell vertrocknen (Salensky, Keller) und dass die Pflanzen aus sonnigen Gegenden pro Flächeeinheit mehr Wasser verdunsten, als diejenigen, welche in beschatteten Orten im Walde sich befinden (Maximoff).

Hier stösst man gleich auf einen Widerspruch: einerseits gibt es viele typische mit den besonderen Lebensverhältnissen der Pflanzen verbundene Merkmale, die bei dem Studium der trockenen Standorte in die Augen fallen, wobei diese Merkmale (z. B. ein Wachsüberzug oder eine Flaumbedeckung) nach den Ergebnissen mehrfacher orientierender Versuche, eine Verminderung des Wasserverlustes durch Verdunstung herbeiführen müssen. Andererseits sind die Xerophyten, welche alle diese Merkmale besitzen und in trockenen Standorten einheimisch sind, gegen die Dürre scheinbar nicht widerstandsfähig.

Demnach zeigt sich in Russland, so wie im Auslande die Neigung (vergl. z. B. E. M. Delf) die ganze Frage über die Xerophyten einer tieferen Analyse zu unterwerfen. Um zu diesem Ziele zu gelangen, muss man nach unserer Ansicht folgende Wege benützen.

Erstens soll man die Merkmale und Eigenschaften der Form und des Baues bei der Pflanze in ihrem Zusammenhange erfassen, die Pflanze als eine lebende Maschine studieren, die nur dann, wenn man das gegenseitige Verhältniss ihrer Teile kennt, begriffen werden kann. Für den Organismus der Pflanze ist es sehr wichtig, dass das Abgeben des Wassers mit Absorption desselben im Gleichgewicht steht. Dieses wird aber durch eine Wechselbeziehung in der Entwicklung der wasseransaugenden und der transpirierenden Organe, den Wegen der Wasserleitung, der Wassergewebe und s. w. hergestellt.

Zweitens soll man die Kraft der in der Wissenschaft erprobten Vergleichungsmethode ausnützen: solche Pflanzenarten müssen verglichen werden, die sich ökologisch schroff entgegenstehen, systematisch aber womöglich eng verwandt sind. Bei gleichem Bauplane werden dann die ökologischen Verschiedenheiten besonders ins Licht treten. Die vergleichende Methode für die Erklärung der ökologischen Besonderheiten war schon seit längerer Zeit benützt worden. Volkens hat sie in einer seiner älteren Arbeiten angewendet, und in späterer Zeit in grossen Masstabe auch Chermeson.

Diese Methode war aber bis jetzt noch nicht in systematischer Weise ausgenützt worden; die quantitative Charakteristik der anatomischen Data, deren Bedeutung für die Klarstellung der Oekologie Salensky hervorgehoben hat, war bisher wenig beachtet worden.

Besonders wichtig ist es aber, nach dem morphologischen und dem anatomischen Studium der Typen von lebenden Pflanzenmaschinen, den Weg der

vergleichenden Physiologie zu betreten und den physiologischen Wert der verschiedenen ökologischen Merkmale in der Pflanzenform und der Pflanzenstruktur festzustellen.

In dieser Richtung sind viele Arbeiten Kolkunoffs über Kulturpflanzen vorhanden. In einer ganzen Reihe seiner in Russland erschienenen Werke ist dieser Forscher zu dem Ergebniss gekommen, dass eine Menge der wichtigsten physiologischen Eigentümlichkeiten der Pflanzen im Gebiete der Assimilation von Kohlenstoff, des osmotischen Druckes des Zellsaftes, der Transpiration u. s. w. in einer korrelativen Abhängigkeit von der Grösse der Zellen und der

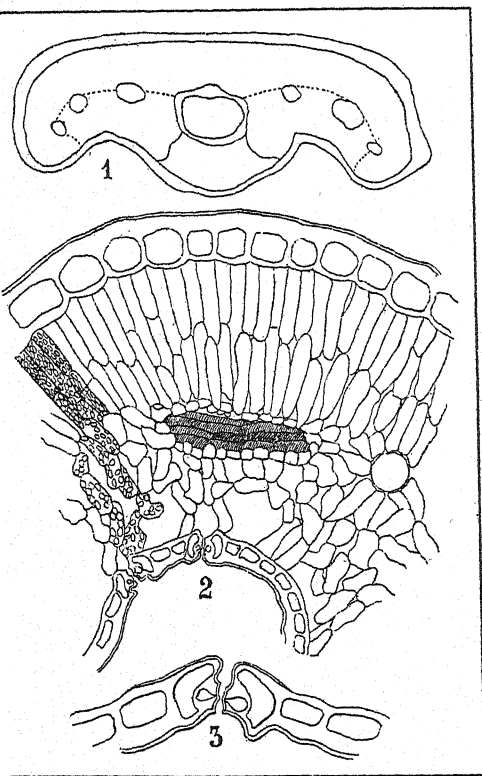


FIG. 8. *Asperula glauca*.

1, 2 und 3 vergrössert resp. 45, 145 und 265.

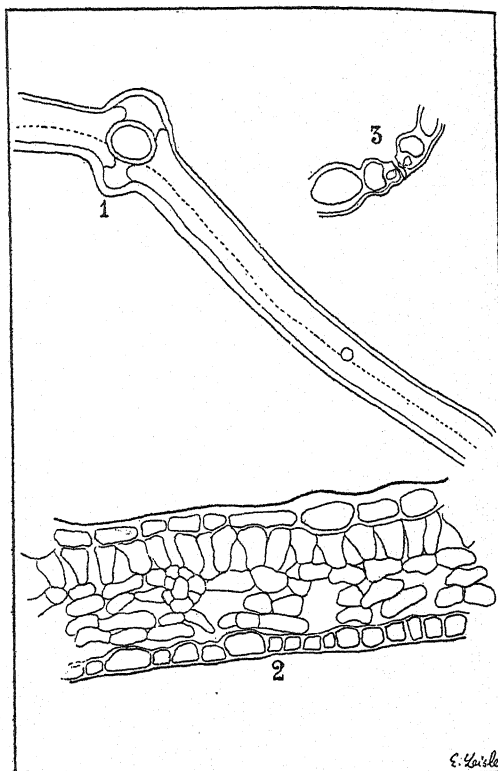


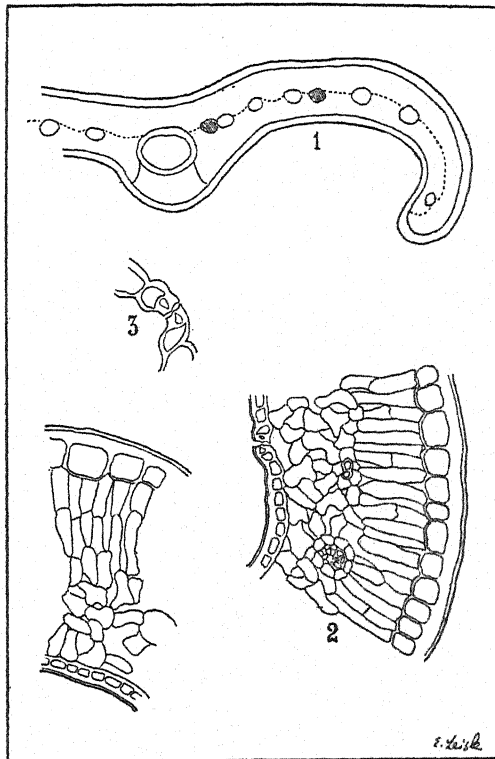
FIG. 9. *Asperula odorata*.

Tabelle XIV.

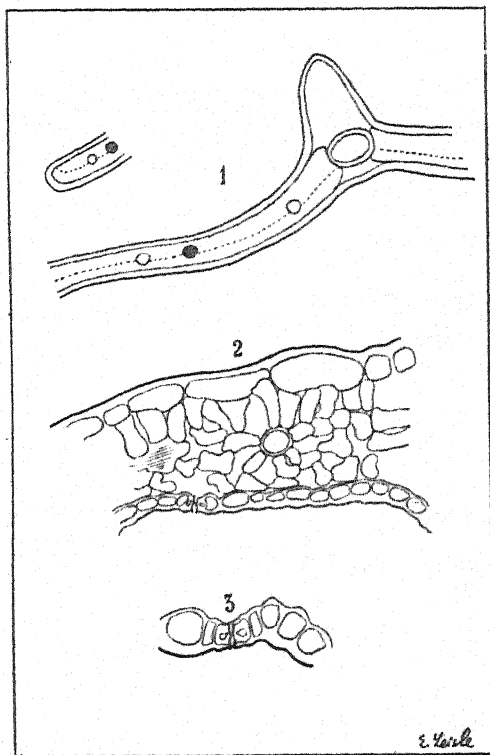
<i>Asperula</i>	Standort	<i>Galium</i>	Standort
<i>glauca</i> Bess.	Steppen, trockene sonnige Kreideentblössungen	<i>verum</i> L.	Steppen, trockener sonniger Sandboden und Kreideentblössungen
<i>tinctoria</i> L.	Steppengebüsche, Saum der Steppenwälder	<i>rubroides</i> L.	Lichte, feuchte überschwembare Wiesen
<i>odorata</i> L.	Schattige Eichenwälder	<i>cruciata</i> Scop.	Schattige Eichenwälder

Die Ergebnisse der quantitativen vergleichend-anatomischen Untersuchungen sind in Tabelle XV wiedergegeben.

Spaltöffnungen stehen. Diese Ergebnisse von Kolkunoff wurden jedoch durch die Forschungen von Jakuschkina und Vavilov über Haferassen nicht bestätigt. Der Grund dieser Widersprüche besteht, wie es mir scheint, darin, dass es noch verfrüht ist die physiologischen Eigentümlichkeiten mit irgend einem einzigen Merkmale der Pflanzenstruktur zu verknüpfen; in diesem Gebiet soll noch eine weite und vielseitige Orientierung geschehen. Die wilden Pflanzen haben für ein solches Studium viele Vorzüge, da zwischen ihnen verschiedenartige und scharf charakterisierte ökologische Typen erwählt werden können.

FIG. 10. *Galium verum*.

1, 2 und 3 vergrößert resp. 45, 145 und 265.

FIG. 11. *Galium cruciata*.

Im folgenden werden wir einige von mir (mit meiner Gehilfin, E. F. Leisle) erhaltene Materialien zu dieser Frage angeben, welche nur einen Anfang unserer Untersuchungen in dieser Richtung bilden.

#### 1. EIN VERGLEICHEND-ANATOMISCHES STUDIUM DER ÖKOLOGISCHEN EIGENTÜMLICHKEITEN EINIGER ARTEN DER ASPERULA UND GALIUM.

Die für das Studium erwählten Pflanzen stammen aus dem Gouvern. Voronesh und nur in einem Falle aus dem Gouvern. Saratov. Angaben über die natürlichen Standorte dieser Pflanze sind aus Tabelle XIV zu entnehmen.



## 2. EIN VERGLEICHEND-PHYSIOLOGISCHES STUDIUM DER TRANSPIRATIONS-INTENSITÄT BEI DEN ÖKOLOGISCH-VERSCHIEDENEN ARTEN VON ASPERULA UND GALIUM.

Zu den Versuchen wurden die unter Wasser abgeschnittene Sprossen mit vollständig entwickelten ausgewachsenen Blättern gebraucht. Es wurden *Asperula glauca* mit *Asperula odorata*, *Galium verum* mit *Galium cruciata* und dann *Asperula glauca* mit *Gal. verum* und *Asp. odorata* mit *Gal. cruciata* u. s. w. verglichen. Der Zustand der Spaltöffnungen wurde mit Hilfe der Infiltrationsmethode kontrolliert. Ueber die Einzelheiten der Versuche vergl. unsere Arbeit in russischer Sprache. Als Illustration wird eine der Tabellen angeführt.

Tabelle XVI.

Der Pflanzenname	Der Versuch war angestellt		Wasserverlust in Milligrammen pro 100 quadr. Centim. Fläche während						Die Transpiration der <i>Asperula glauca</i> als 100 angenommen		
	Datum	Bedingungen	15 Min. 1-34	15 Min.	30 Min. -2-34				30 Min. 1-34	30 Min. -2-34	30 Min.
<i>Asperula glauca</i> <i>odorata</i>	5. vi.	Im Vegetationsgehäuse bei diffusum Licht	166 42	135 57	364 114	—	—		100 32	100 31	—
<i>Asperula glauca</i> <i>odorata</i>	5. vi.		—	—	15 Min. 2-30 113 49	15 Min. 150 73	30 Min. -3-30 263 146	30 Min. 2-30 100 46	30 Min. -3-30 100 56	—	—
<i>Asperula glauca</i> <i>odorata</i>	13. vi.	Daraussen in der Sonne	15 Min. 10-34 279 140	15 Min. 314 148	30 Min. 697 270	30 Min. -12-04 836 288	—	30 Min. 10-34 100 41	30 Min. -12-04 100 39	100 34	—

Im Allgemeinen waren folgende Resultaten erzielt worden.

1. Die Steppenarten zeigten eine weit grössere Transpirationsintensität, als die Wald- (Schatten)arten; der Unterschied war ziemlich beständig und die Intensität verhielt sich etwa wie 100 zu 30–50.

2. In Hinsicht der Transpirationsintensität, wie auch der anatomischen Eigenschaften, verhält sich *Galium verum* zu *G. cruciata* ungefähr so, wie *Asperula glauca* zu *A. odorata*.

3. *Asperula tinctoria* nach ihrer Transpirationsintensität, wie nach ihren anatomischen Merkmalen, nahm einen Platz zwischen der *Asperula glauca* und der *A. odorata* ein.

Unsere Versuche weisen kurz gesagt auf einen wunderbaren, fast mathematischen Parallelismus zwischen der Transpirationsintensität und den anatomischen Eigenschaften der Pflanze, und dieser Parallelismus ist naturgemäss als eine Abhängigkeit der Funktion vom Bau zu deuten.

In letzterer Zeit lässt sich eine Tendenz bemerken den anatomischen Merkmalen alle Bedeutung für die Bestimmung der Widerstandsfähigkeit gegen die Dürre und der Xerophilie der Pflanzen abzusprechen.

Diese Verneinung erscheint uns als voreilig; im Gegenteil man sollte doch den physiologischen Wert der anatomischen Charakterzüge ergründen.

Eine bemerkenswerte Uebereinstimmung der Vergleichungszahlen für die Länge der Nerven pro Flächeneinheit und der Transpirationsintensität bei einander entgegengestellten Arten von *Asperula* und *Galium* lässt sich erkennen. Diese Uebereinstimmung wird durch Tabelle XVII beleuchtet; diese Tabelle enthält auch einige Data zur Erläuterung der angegebenen Ergebnissen.

Tabelle XVII.

	Vergleichende Länge der Nerven pro Einheit der Oberfläche der Blätter	Vergleichende Transpirationsintensität					
		100	100	100	100	100	100
<i>Asperula glauca</i>	100	100	100	100	100	100	100
<i>Asp. tinctoria</i>	66	—	—	—	—	81	67
<i>Asp. odorata</i>	33	32	31	46	56	54	54
<i>Galium verum</i>	100	100	100	100	—	—	—
<i>G. cruciata</i>	37	46	33	53	—	—	—

Wir müssen jedoch diese Uebereinstimmung nicht überschätzen: das Entsprechen der Struktur und der physiologischen Eigenschaften sollte noch bei verschiedenen Pflanzen, und in verschiedenen Richtungen beleuchtet werden. Zum Schluss will ich noch einige Bemerkungen über die Spaltöffnungen anführen.

Bei unseren Versuchen über die Transpiration haben wir mehrmals den folgenden Umstand angetroffen: die zu dem Versuch genommenen Triebe transpirierten am Anfange sehr schwach. Es fand sich in diesen Fällen, dass die Spaltöffnungen derjenigen Pflanzen in der Anstalt, von denen man die Triebe abgeschnitten hat, schon geschlossen waren. Deshalb wurde der Stand der Spaltöffnungen bei dem Aufstellen des Versuches schon in der Anstalt kontrolliert. Bei allen Versuchen, die hier beschrieben sind, stammen die Sprossen von Pflanzen mit offenen Spaltöffnungen ab.

Der Sommer von des J. 1922 war anfangs feucht und kühl; die Pflanzen in der Anstalt waren verzärtelt. Als nachher sehr heisse Tage auftraten, so schlossen einige von diesen verzärtelten Pflanzen die Spaltöffnungen schon am frühen Morgen.

Diese Erscheinung äusserte sich besonders scharf bei unseren Exemplaren des *Galium verum*. In der zweiten Hälfte des Tages konnten die Versuche mit dieser Pflanze nicht vorgenommen werden. Manchmal waren die Spaltöffnungen bei dieser Pflanze schon um 11 v. Mitt. geschlossen.

Eine besondere Reihe unserer Arbeiten bilden die vergleichenden Versuche über das Austrocknen derselben Arten von *Asperula* und *Galium*. Hier treffen wir wieder ein eigentümliches Verhalten der Spaltöffnungen bei den verschiedenen Arten an. Z. B. bei *Asperula glauca* blieben die Spaltöffnungen bei Licht offen, selbst bei einer starken Vertrocknung. Es ist möglich, dass das schnelle Vertrocknen einiger Xerophyten mit dieser Befähigung verbunden ist. Ueber diese Versuche gedenken wir in einer besonderen Arbeit Mitteilung zu machen.

## SCHLUSSBEMERKUNGEN.

In der vorhergehenden Auseinandersetzung haben wir diejenigen Wege und Mittel besprochen, durch welche die wilden Pflanzen nicht nur die ungünstigen äusseren Bedingungen ertragen, sondern auch die ihnen feindlichen Naturkräfte zu ihrem Nutzen anwenden.

Wenn man in den, durch Versalzung umgekommenen Baumwollensplantagen Turkestans, die ausserordentlich üppig sich entwickelnden sukkulenten Salzpflanzen beobachtet, so taucht wohl der Gedanke auf, ob es nicht möglich wäre, solche Rassen der Baumwollpflanze ausfindig zu machen, bei denen die grosse Salzhaltigkeit auf die Entwicklung stimulierend wirken würde. Dass dieser Gedanke keine blosser Utopie ist, wird dadurch gezeigt, dass in demselben Gebiet sich eine Form der Baumwollpflanze mit etwas sukkulenten Blättern und einem erhöhten osmotischen Druck findet. Es scheint als ob die Natur damit beginnt eine für Salzböden geeignete Rasse der Baumwollpflanze zu erschaffen.

Bei einem unserer Versuche haben wir eine Kultur des *Phaseolus* stark versalzt, indem die Konzentration NaCl im Substrat auf 1 % vom gesamten Wassergehalt gebracht wurde.

*Phaseolus* warf seine Blätter rasch ab, während die Wasserdrüsen eine Flüssigkeit mit einem grossen Gehalt an Kochsalz ausschieden. Hiermit ist wieder der Gedanke verbunden, ob es nicht möglich wäre, bei *Phaseolus* eine solche Rasse zu finden, welche ihr Leben auf ziemlich salzhaltigen Standorten, nach dem Typus jener Halophyten, welche grosse Mengen leichtlöslicher Salze ausscheiden, verbringen kann.

Wir wollen damit sagen, dass für die Förderung der Pflanzenzucht unter neuen Bedingungen, wohl auch neue Wege auf der Basis eines ökologischen Studiums der wilden Pflanzen zu suchen sind.

Die Landwirtschaft arbeitet bis jetzt nur mit wenigen ökologischen Typen. Man muss noch neue ökologische Typen von Kulturpflanzen ausfindig machen und untersuchen.

Ueber die Einzelheiten der Versuchsaufstellung u. s. w., mit Hinweisungen auf die Literatur siehe folgende unsere Arbeiten in russischer Sprache.

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2. **B. A. Keller und E. F. Leisle.** "Die Pflanze als lebende Maschine." *Ibid.* 1922.
3. **B. A. Keller.** "Zur Erklärung der Oekologie derjenigen Salzpflanzen, welche die Salze nach aussen hin ausscheiden. Versuche mit *Frankenia pulverulenta* L." (Bald im Druck zu erscheinen.)

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\* Alle diese Arbeiten sind geschrieben in russischer Sprache.

† Ausser anderen Arbeiten in den letzten Jahren.

## ENGLISH SUMMARY.

The object of the paper is to summarise the results of researches on the form, structure, and ecology of certain wild species of plants inhabiting the dry regions of south-eastern Russia in order to obtain indications as to the best culture plants to grow in these regions, at present hardly invaded by agriculture on account of the drought and high salt content of the soil.

I. *SALICORNIA* HERBACEA.1. *Transpiration and drying.*

The highly salty soils (mostly NaCl and Na<sub>2</sub>SO<sub>4</sub>) are often associated with high water content, owing to a high water table. Two halophytic types occur in such regions: (a) succulents with much salt in their cell-sap, (b) non-succulents which excrete salt in considerable quantity. The glasswort is a good representative of type (a): it is often a pioneer on salty ground. In spite of work by many investigators we are still far from understanding its ecology.

Plants cultivated without NaCl showed a high and even transpiration. This diminished as the salt was increased, was still fairly high with 1 % NaCl, but quite insignificant with very high concentrations. Transpiration diminished at the time of flowering, but this is less important to the plant. The plant absorbs far less salt than water. In a 3 % culture solution a plant transpired enough water to raise the salt percentage of its body to 70 if it had absorbed the solution as it stood: in fact the percentage of salt in the body does not exceed 1 to 2. In a 5 % culture solution the transpiration curve is very similar to that in a 1 % solution, but the transpiration at night is diminished.

Assimilating shoots cut off from the roots show the same variations in drying out as transpiring plants; in the first few minutes they lose water at about the same rate. Plants grown without salt lose water much quicker than those grown in salt solutions. From these results it appears that plants grown in salty water show a much greater resistance to water loss than those grown without salt. They also show a high osmotic pressure, and this may well be the cause of their resistance to water loss. The influence of salt also brings about the succulence, the strong development of water tissue and the decrease in the number of stomata per unit surface (Batalin, Lesage, and others).

2. *Development of Salicornia in relation to the degree and kind of salinity.*

The plants were grown in sand cultures saturated with a solution of nutritive salts, to which were added sodium and potassium salts in equimolecular proportions to sodium chloride, with controls. The results showed that *Salicornia* grew best in a medium degree of salinity. In normal nutritive solution the plants remained backward in growth, had very thin assimilating joints of an intense green colour, and an increased transpiring surface per

unit volume. On the addition of certain salts the plants grew as they do in their natural habitat. The sodium salts have a stronger effect than the potassium, the chlorides than the sulphates. The greatest effect is produced by sodium chloride in medium concentration (0.8 % of the water used in the sand cultures, 1 % in the water cultures produced a more luxuriant development than the wild plants showed). The curve of development falls on each side of this optimum concentration of NaCl. The curve of *succulence*, however, continues to rise with increased concentration of NaCl. A marked increase in succulence was obtained with a small addition of Na or K salts to the nutritive solution (1 gr. of NaCl or 1.3 gr. KCl to the 4 gr. of mixed nutritive salts which each vessel contained). In higher proportion (12.8 gr.) KCl worked differently from NaCl, producing no further heightening of growth and even some reduction; while in very high proportions KCl produced much weaker growth than an equimolecular quantity of NaCl. The highest proportion of KCl (64 gr. per vessel) produced partial death of the plants.  $\text{Na}_2\text{SO}_4$  promotes growth, luxuriance and succulence, but much less than NaCl. In comparison with the other salts  $\text{K}_2\text{SO}_4$  has a relatively weak stimulating effect on the plants. A high K-content of the substratum probably has a toxic effect. The author must therefore qualify his agreement with Bernatsky that the *kind* of salt has little influence on halophytes, but we may suppose that KCl may form salty soils with typically developed *Salicornia*.

Plasmolysis tests show that luxuriant plants raise their osmotic pressure but little or not at all. It is only when there is strong suppression of growth by salt supply that the osmotic pressure is considerably raised. Up to a certain point increased osmotic pressure seems to be an internal factor promoting growth, and if growth is proceeding with a certain intensity osmotic pressure does not rise too high. It was found that increase of growth, succulence and osmotic pressure, through addition of NaCl, also took place when transpiration was almost suppressed in a glass chamber.

Cells which attain greater dimensions as a result of the supply of salt also show larger cell-nuclei.

### 3. *Salicornia herbacea* in its natural habitats.

Fitting's criticism of Schimper's views on the xerophytic nature of halophytes, and especially his statement that the accumulation of salts in the plant is wholly independent of transpiration and depends solely on a peculiar character of the plant such as the permeability of its protoplasm, cannot be wholly accepted. Fitting left out of account the different layers of soil to which the roots of different species penetrate. For instance, in the deserts of Turkestan the roots of *Alhagi camelorum*, which undoubtedly has a high transpiration, penetrate to fresh water below the salty surface soil. At the same time Schimper's statements amount to no more than a preliminary formula and require detailed working out for individual species under their natural con-

ditions. *Salicornia herbacea* is a water-loving halophyte and at germination almost a water plant. The seed germinates normally in a weak salt solution, and very well in distilled water, though fairly well in a 2 % solution of NaCl. After germination its growth is stimulated by salt and thus it uses the spring season when the soil is rich in water and the salt content moderate. The osmotic pressure remains relatively low, the salt which is accumulated being distributed through an increasing tissue mass (cf. Schimper's view that the water tissue protects the assimilating tissue from excessive accumulation of salt). In the hot dry summer the salt content of the substratum passes the optimum for the growth of the species, which is checked, large quantities of salt are accumulated and the osmotic pressure rises, preventing over-transpiration of the assimilating cells, though there is still a daily rhythm of transpiration which affords a certain protection of the surface from overheating. The absolute quantity of water absorbed is small. Later the green fleshy cortex loses its chlorophyll, dries and is cast off, this process progressing upwards from the base of the main stem to the branches, at the period of flowering and fruiting. This description is illustrated by examples of plants growing in different conditions. The author holds that if a given character is submitted, through the influence of external conditions, to a constant one-sided modification, a heritable alteration in the same sense can arise by an effect on the corresponding gene. Though it is a highly specialised form of salty soils the glasswort retains a high plasticity in this respect, and it is possible that the fixed hereditary quality is only a great flexibility, a capacity for becoming succulent under the influence of salt and a quick response under the influence of relatively weak concentrations of NaCl and KCl.

If the seeds of the glasswort fall on a very damp but not salty spot, the plants grow weakly, develop little succulence, are badly protected against drying, and are suppressed by other plants. In correspondence with the reduction of surface the plant is light-loving.

## II. FRANKENIA PULVERULENTA L.

This little annual is a good example of a halophyte of type (b), which excretes great quantities of the easily soluble salts. Type (b) is well represented in S.E. Russia by *Frankenia pulverulenta*, *F. hirsuta*, *Tamarix Pallasii* and *hispida*, *Statice caspia*, *tomentella*, *otolepis*, *perfoliata*, *Cressa cretica*, *Aeluropus litoralis* and *repens*. They inhabit places with good salt and water supply, and act to a certain extent as pumps, raising the easily soluble salts from the deep to the surface layers of soil.

Rühland's work, mainly on *Statice Gmelini*, besides other valuable results, has given a good experimental foundation for the view that the copious excretion of salts has the function of freeing the living cells from a superfluity of them. Our experiments have shown that *Frankenia* is not, like *Salicornia*,

strengthened by a supply of salt. Addition of 0.1, 0.5 or 1.0 % NaCl gave luxuriant growth, scarcely differing from that in the normal nutritive solution without addition. With 3 to 5 % NaCl a considerable suppression of growth occurred, while in higher concentrations still the plants do not wilt easily, the leaves remain fresh and the osmotic pressure is notably raised. The little drops of water on the plant are derived mainly, or almost exclusively, from the interior of the plant. Condensation of water from the air during a whole night in the moist chamber is inconsiderable, but gains in amount with increase of salt. The excretion of liquid from the plant is much greater in the plants supplied with salt so long as the salt does not reach too high a concentration. The excretions of easily soluble salts are to be regarded as an external osmotic mechanism which sucks water from the interior of the plant. If the excreted water is sucked away with blotting paper, the power of the plants with a salt supply to excrete water is greatly lessened. But this power is in great measure restored if the plant is sprayed with a solution of common salt and the newly excreted drops allowed to dry so that a salt incrustation remains on the surface. An extraordinarily great excretion of liquid can also be obtained from cultures which have had no salt supplied to them by spraying with salt solution and subsequent drying off of the drops, and the same result can be obtained by sprinkling powdered NaCl on the cut off shoots of *Frankenia* which have had no salt supplied to them but have been placed with their cut ends in distilled water.

### III. THE PLANT AS A LIVING MACHINE.

It has recently been shown that many plants with the characters of xerophytes dry out easily and quickly (Salensky, Keller), and that plants from sunny habitats evaporate more water per unit surface than those of shady places in woods (Maximoff). The contradiction appears that many plants conspicuous in dry habitats have such characters as wax covering or pubescence which must diminish evaporation, and yet xerophytes which possess all these characters are apparently not resistant to water loss. It is necessary in order to resolve such contradictions to study the whole plant as a living machine. It is very important for the plant as a whole that absorption and loss of water should be in equilibrium. This is brought about by the mutual relations of the absorbing and transpiring organs, the water channels, water tissue, etc. Species which are sharply contrasted ecologically but closely allied taxonomically should be compared. The ecological differences will be illuminated by the common plan of construction. This method has not hitherto been systematically used: little attention has been paid to the quantitative characterisation of anatomical data. The physiological value of various ecological characters of form and structure have to be established.



1. *Comparative anatomical study of the ecological peculiarities of certain species of Asperula and Galium.*

The data obtained show a quite surprising, almost mathematical regularity of quantitative anatomical characters. The woodland and steppe species are moulded as if by a stamp, repeating the same features on different but parallel evolutionary paths. In the steppe species the stomata are much more numerous than in the woodland ones and they tend to be distributed on the upper sides of the leaves. The approximation of the ecologically corresponding species of the two genera is expressed in the anatomical structure of leaf and stem. Apart from the characters given in the table, the xeromorphism of the steppe species is expressed by their leaves assuming an acicular form and by their edges being rolled downwards. The green tissue (and the whole leaf) is much thicker, a fact which perhaps demands an increase of the stomata per unit surface. The palisade tissue is strongly developed and the cuticle is thick. A physiological regularity must naturally correspond with this regularity in form and structure, and this is shown in the next section. Single narrow taxonomic groups have limited definite paths of ecological evolution. The two genera in their adaptation to the external conditions of wood and steppe use the same means. The ecological approximation corresponds with the phylogenetic in spite of the difference of floral structure, so that the ecological evolution of the nutritive organs crosses the evolution of the flower in a remarkable way. The close resemblance of *Galium* and *Asperula* has often been noticed. In Australia *Asperula geminifolia* and *Galium geminifolium* are closely similar, and are distinguished only by the stiff spreading growth and the corona characteristic of *Galium*.

2. *Comparative physiological study of the intensity of transpiration in ecologically different species of Asperula and Galium.*

Shoots cut off under water and with completely developed leaves were used. *Asperula glauca*, *A. odorata*, *Galium verum* and *G. cruciata* were compared in pairs. The following results were obtained. The steppe species show a far greater transpiration than the woodland species. The distinction is fairly constant and the ratio 100: 50-30. Both in transpiration and anatomical characters *Galium verum* bears the same relation to *G. cruciata* that *Asperula glauca* does to *A. odorata*. *Asperula tinctoria* lies between the other two both in transpiration and anatomical structure. The remarkable, almost mathematical, parallelism between transpiration and structure clearly indicates the dependence of the function upon the structure which it has been the fashion recently to ignore—almost to deny. Any such denial is at least premature. It is necessary, on the contrary, to evaluate the physiological value of anatomical characters. There is a notable correspondence between the comparative numbers for the total lengths of the veins per unit surface in the

contrasted species of *Asperula* and *Galium*, but its value should not be overestimated.

The stomata of shoots cut off for transpiration work were sometimes found to be closed, so that transpiration was at first very weak, and the delicate plants produced in the damp and cool early summer of 1922 closed their stomata very early in the day when hot dry weather came on. All the experiments recorded in the table were carried out with plants whose stomata were open. In the experiments on drying out of the shoots of *Asperula glauca* the stomata remained open in light, even when strongly dried.

#### CONCLUDING REMARKS.

In this investigation it has been shown how plants not only protect themselves against the unfavourable influences of their environment, but even turn them to their advantage. By the study of the ecology of wild plants in environments similar to those in which cultivated plants are to be grown, it should be possible to discover races which are thus capable of meeting special unfavourable conditions, and to extend the study to different pure strains of cultivated plants. Several indications of the sort have been met with in the course of the work. In this way we should be able to widen the now very narrow range of varieties in cultivation and to obtain much better results under various conditions of life.

# THE AERIAL SURVEY OF THE IRRAWADDY DELTA FORESTS (BURMA)

NOTES EMBRACING THE OBSERVATIONS OF MESSRS A. W. MOODIE,  
C. R. ROBBINS AND C. W. SCOTT, COMPILED AND EDITED  
WITH PERMISSION

By L. DUDLEY STAMP, *University of Rangoon.*

(*With Plates VII—XII and three Illustrations in the Text.*)

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## I. INTRODUCTORY NOTE.

THE notes which follow are in the nature of a Review. It sometimes happens that work of immense value to the ecologist and the botanist is hidden away in official publications dealing primarily with other matters. In the present instance the official writings concerned are not even accessible to the general public and the writer is much indebted to Mr F. A. Leete, C.I.E., late Chief Conservator of Forests, Burma, and to Mr C. B. Smales, Chief Conservator of Forests, Burma, for permission to extract and publish the information given below. The writer claims no personal share in the work; it is a compilation of the observations of the following officers of the Forest Service in Burma: Mr A. W. Moodie, M.A., Mr C. R. Robbins, B.A., M.C., and Mr C. W. Scott, B.A. Major R. C. Kemp, who was in charge of the actual survey, kindly took much trouble in providing the photographs with which this paper is illustrated and in helping the writer to select representative ones.

## II. HISTORY OF THE SURVEY.

The tidal forests of the Irrawaddy Delta have long been a valuable source of timber and fuel for the towns and villages of the rich rice-growing regions of the Delta. The most valuable tree is the Kanazo (*Heritiera fomes*) which may reach a height of 150 ft. It will be obvious at once that the tidal forests are very different from the mangrove swamps which here occur as fringes, but which elsewhere may form the principal vegetation of tropical deltas. In

order to protect them from ruthless exploitation and destruction the more important of the tidal forests were formed into Government Forest Reserves between 1895 and 1901. In the majority of cases the Forest Reserves in India and Burma are mapped by the Survey of India on the scale of 4 ins. to the mile. Armed with these topographical maps the Forest Officers then prepare a report on the arboreal vegetation (with special reference to exploitable species) of the forest (which is divided into "compartments") and draw up a scheme of exploitation consistent with continuous regeneration. The report and scheme is known officially as a "Working Plan" and is usually accompanied by a rough "stock map" showing the distribution of the valuable types of forest or forest species.

In the case of the tidal forests of the Delta, a topographical survey was extremely difficult, if not impossible, and remained unaccomplished. An adequate examination of the vegetation was almost equally difficult—the most the Forest Officer could do was to cruise through all the creeks which would admit a small launch and to make occasional excursions into the indescribably filthy mud of the forest itself at low tide. It happens, however, that the creeks are often fringed with forest of a very different type—in fact with almost useless mangrove swamp—and it is a matter of guesswork to attempt to estimate what lies behind. Some years ago (1916) doubts were expressed as to the value of much of the reserved forest and proposals were set on foot to abandon a large part. Without proper investigation such a course was obviously unwise and to Mr A. W. Moodie fell the task of drawing up a Working Plan. Without maps—except incomplete small scale ones—Mr Moodie set to work and has produced an encyclopaedic Working Plan, which apart from being a mine of information on the tidal trees of Burma is a monument of industry under difficulties<sup>1</sup>. Mr Moodie's work proved conclusively the value of the forests and the need for a more detailed survey. After preliminary negotiations a contract was signed on July 26th, 1923, between the Government of India and Major R. C. Kemp for an aerial survey of about 1000 square miles of reserved forest. The aerial survey was undertaken primarily for the construction—by the Survey of India—of 4-inch-to-the-mile maps. Many of the provisions in the schedule to the contract are to that end, notably the time of day at which photographs were to be taken. The use of the aerial photographs in vegetation survey was unknown and was given a somewhat secondary consideration, though the schedule stipulated that photographs were to be submitted to enable the Forest Officer to construct a stock map. Major Kemp commenced work in January, 1924, and by the end of March the photo-mosaic was complete. During the course of the work two Forest Officers—Messrs C. R. Robbins and C. W. Scott—flew over repre-

<sup>1</sup> *Working Plan for the Forests of the Irrawaddy Delta, Burma, 1924-5.* Under a recent order of Government a few copies of Working Plans are, in the future, to be placed on sale to the public at the Government Book Depot, Rangoon. The present Plan will be available in this way.

sentative tracts of ground. With their kind permission the substance of their observations will be given below.

### III. THE AERIAL SURVEY.

Major Kemp established his hydroplane base at Monkey Point, Rangoon, where all photographic work was also carried out. From Rangoon to the furthest point surveyed is about 120 miles (see Fig. 1). Hydroplanes were, of course, used.

According to the schedule to the contract the work could be performed using either

- (a) a 7 in.  $\times$  7 in. negative with a 10-in. F.L. lens to be exposed at a height of not less than 12,000 ft., giving a scale for the photographs of 4.4 ins. = 1 mile and each negative covering 2.5 square miles; or
- (b) a 5 in.  $\times$  4 in. negative with an 8-in. F.L. or 6-in. F.L. lens to be exposed at a height of not less than 10,000 ft. or 13,300 ft. respectively, giving a scale for the photographs of 3.17 ins. = 1 mile and each photograph covering 2 square miles.

Actually, however, all photographs were taken from a height of 10,000 ft., quarter-plate negatives being used and the actual scale obtained being 3.3 ins. = 1 mile. Departure from mean height at which a series of photographs was taken was not allowed to exceed 1 per cent. or 100 ft. in 10,000. Special precautions were taken to avoid tilt, which, it was stipulated, should not exceed 2° in 75 per cent. of the photographs and in no case to exceed 3°. The overlaps for the photographs, both lateral and forward, was to be 30 per cent., or not in any case less than 20 per cent.

For experimental purposes a number of photographs were taken from a height of 5000 ft., but it was found that no more detail was visible than in enlargements from photographs taken at 10,000 ft.

In order that narrow creeks should not be masked by shadows the Survey of India stipulated that all photographs should be taken between the hours of 10 a.m. and 3 p.m., when shadows are short. As will be noted in the sequel photographs taken before or after those hours are more valuable in the construction of a vegetation map as length of shadow affords some conception of the relative height of vegetation. The value of oblique photographs taken from lower levels, for the same purpose, was not appreciated till somewhat too late in the work (compare Pl. XI).

Panchromatic plates were used. Mr Robbins expressed a slight disappointment that the varying shades of green did not come out well but the photographic expert doubted whether the use of orthochromatic plates would have been beneficial.

## IV. PLANT SUCCESSION IN THE IRRAWADDY DELTA.

Before proceeding to an interpretation of the aerial photographs it will be advisable to summarise what is known of plant succession and vegetation types in the Irrawaddy Delta. Colonel English, an officer of Government who took much interest in the Delta Forests, drew up a classification of vegetation after having toured through the Delta Reserves in the latter part of 1916. His *Note on Mr Lawrence's Report on Disafforestation of parts of the Irrawaddy Delta Reserves* (printed for Government on February 24th, 1917) contains many facts of interest and considerable lists of plants. It is to Mr Moodie, however, that a more exact description is due and the following account is summarised from his observations.

A casual glance at a map of Burma will show that the Irrawaddy River commences to give off distributaries about the latitude of Henzada ( $17^{\circ} 40' N.$ ) and finally the waters of the river empty themselves into the sea through a number of mouths stretching from the Bassein River on the west to the Hlaing or Rangoon River on the east (see Fig. 1). The main flow of fresh water, however, passes down the Eya River and neighbouring waterways. Very little water indeed passes down the Bassein River and the distributaries in the west of the Delta, such as the Ywe. It follows, therefore, that the rivers and creeks in the western part of the Delta are filled mainly with salt water, the distributaries in the centre and towards the east with fresh or brackish water. The Irrawaddy has only one flood season; rising rapidly in May and June—when the monsoon breaks—to a maximum about August and then commencing to fall, the lowest water being reached about March or April in the height of the hot season.

With two exceptions the whole of the seaward half of the Delta—the area now under consideration—is flooded by spring tides during the rains or high water season and much also by neap tides at other seasons. The two exceptions are firstly the sandy ridges along the sea face—dune sand thrown up by the waves—which rise to 3 or 5 ft. above the general level and secondly the Myaungmya ridge which rises in places to 120 ft. above sea level. The latter, like the ridge on which part of Rangoon stands, is also certainly of tectonic origin, though the Tertiary rocks of which it probably consists are masked by lateritisation and covered by sandy or even gravelly soils. Apart from these two exceptions the level of the Delta does not vary more than a few inches, and the formation is entirely alluvial.

The water of the Irrawaddy is never clear, it carries vast quantities of silt and mud. Deposition takes place both in the Delta and out to sea and deposition seems to be greatest when a rough equality between the volume of fresh and the volume of salt water is reached. Deposition therefore takes place lower down the channels in the high water season and also lower down those channels in which the water is comparatively fresh.

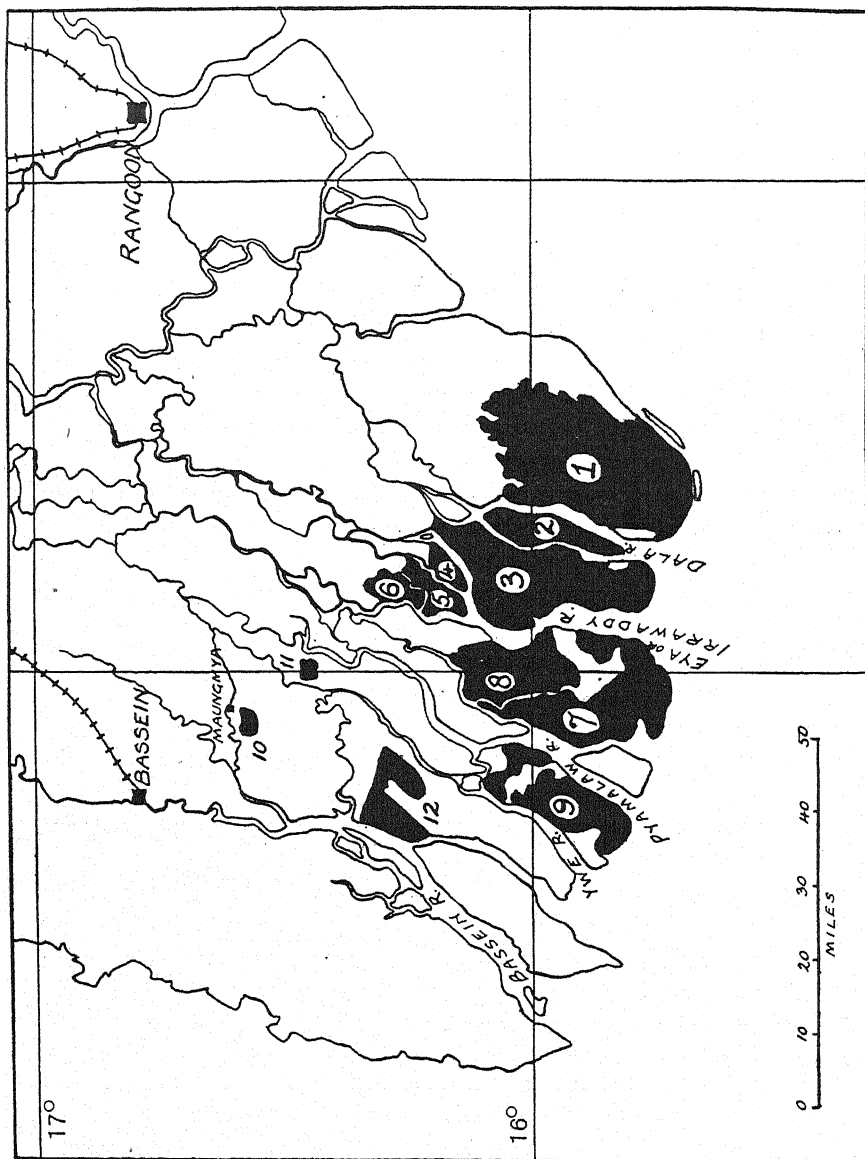


FIG. 1. The Forests of the Irrawaddy Delta.

Government Reserved Forests in black:—1 = Pyindaye Reserve; 2 = Meimahla Res.; 3 = Kandonkani Res.; 4 = Nyaung Res.; 5 = Kalayaik Res.; 6 = Labatkwe Res.; 7 = Pynalan Res.; 8 = Kakayan Res.; 9 = Kyagan-Kwinbank Res.; 10 = Kyaukkon Res.; 11 = Ngayabo Res.; 12 = Lebyauk Res. 10 and 12 are situated on a ridge and are mainly non-deltaic.

According to Moodie the new deposit of mud as soon as it is exposed during low tides affords a foothold for vegetation. Grasses appear first and help to collect more silt and also floating seeds, especially those of Kambala (*Sonneratia apetala*). The spreading roots of this tree collect silt and the level rises till the Kambala is killed and Kanazo (*Heritiera fomes*) takes its place. It would seem that certain more vigorous specimens of Kambala survive and form big trees in the midst of Kanazo Forest. When tidal land has been

formed in this way, the perimeter is raised by continued deposition, whilst the inside may be lower and flooded by every tide. Near the sea the vegetation may be killed by sand thrown up by the waves.

From the fact that the coarser silt will be deposited first it follows that the soils in the northern part of the Delta forests are more loamy than further south, where stiff clay predominates. The latter may sometimes be observed to dry and crack during low tides, and supports a comparatively poor vegetation.

From what has been said it is obvious that level and salinity are the controlling factors in the distribution of vegetation. Very little damage is caused by wind, and cyclones are unknown.

The classification of the conditions and vegetation proposed by Mr Moodie is as follows:

- A. Not flooded at any time.
  - (i) Inland sandy levels—slightly higher than (ii) and trees with roots in fresh water.
  - (ii) Sandy levels near the sea face—trees with roots in salt water.
- B. Flooded only during the rains.
  - (iii) Clay high levels—flooded with water mainly fresh.
- C. Flooded during spring tides.
  - (iv) High intermediate levels—flooded with water, mainly salt.
- D. Flooded during all tides (i.e. covered at high tide).
  - (v) Low intermediate levels.
  - (vi) Low levels flooded with water mainly fresh.
  - (vii) Low levels flooded with water mainly salt.

The vegetation corresponding to each of the above set of conditions is as follows:

- (i) **Inland sandy levels**, not flooded at any time. The flora is characteristic of the ordinary hill or plains forest and has little specially distinctive of tidal forest. Owing to the high rainfall of the Delta region (90 ins. to 120 ins.) the vegetation is a variety of the Evergreen Dipterocarp Forest which covers all the wetter regions of Burma (type L 1 of Stamp, *The Vegetation of Burma*, 1924). These inland sandy levels often occupy only a few acres and may rise as islands in the midst of the tidal Kanazo Forest; they are frequently cultivated, as fresh drinking water is usually available.
- (ii) **Sea face sandy levels** or region of Dune Forests. Wherever the sea has thrown up a line of low sand hills there is usually a wide grassy area with *Ipomaea pes caprae* and *Canavalia obtusifolia* (*Ipomaea-Canavalia Association*). Some 300 or 400 yds. back from the sea face may be older beaches or dunes with tree growth. On similar positions (i.e. dunes) round the coasts of Arakan, Tenas-



serim, Malay Peninsula and most of the islands of the East Indies are found the *Casuarina* Dune Forests (*Casuarina equisetifolia* consociations, Type L 22 a of Stamp, *Vegetation of Burma*). In the present case, however, *Casuarina* is absent and the trees commonly present on the ridges are *Albizia procera* (sit), *Grewia microcos* (myatya) and *Eugenia* spp. (thabye), together with a tall grass.

- (iii) **Clay high levels** (known to the Burmans as "Kon-byaik," i.e. high scrub). Such areas, being flooded only during the rains and then by fresh water, are characterised by the absence of the typically tidal Kanazo tree (*Heritiera fomes*), i.e. the ground has risen above the level for Kanazo. Such areas are covered either by (1) scrub forest or (2) grass. Tree growth is scattered and poor, whilst the undergrowth is thick and difficult to penetrate, consisting of a tangle of canes. Certain members of the undergrowth, notably *Hibiscus tiliaceus* (thinban), may form a densely matted consociation with no trees. Trees include thitpyu and myauk-on (*Lauraceae*), *Elaeocarpus hygrophilus* (panmauk-kon), *Calophyllum* sp. (talapi), *Litsaea* sp., *Eugenia* sp., *Lagerstroemia* sp., *Mangifera* sp., *Diospyros* sp., and *Amoora cuculata*. Undergrowth includes *Calamus erectus*, *Phragmites* sp., *Pinanga* sp., *Clinogyne dichotoma*, *Flagellaria indica*, *Calamus arborescens* and *Hibiscus tiliaceus*.

- (iv) **High intermediate levels.** Such regions are occupied by the highest of the true tidal forests. Trees like Kanazo which are characterised by "tent-peg" aerial roots (respiratory roots or pneumatophores) rising up through the tidal mud are present, but their aerial roots are very short.

Where the water is mainly fresh the higher intermediate levels are characterised by large old Kanazo (*Heritiera fomes*)—i.e. it is near the upper limit for this species—*Pandanus foetidus*, *Litsaea* sp., and *Amoora cuculata*, together with *Cynometra ramiflora* and patches of *Calamus*. *Cynometra ramiflora* (myinga) may occur as consociations forming "myinga byaik."

When the water is more salt, Kanazo occurs with an understorey of *Cynometra ramiflora* and sometimes *Ceriops roxburghiana*, whilst the ground is covered with *Acrostichum aureum*. In places consociations of *Hibiscus tiliaceus* occur. As these lands are only flooded a few times during the year and then with salt water, evaporation at other times results in a concentration of salt in the surface layers so that the ground becomes impregnated with salt and affords the main reason for the poverty of tree growth.

- (v) **Low intermediate levels.** The largest and most valuable of all the tidal trees of Burma—Kanazo or *Heritiera fomes*—flourishes best where the land is flooded daily by the tide but where the

waters disappear completely from the surface for several hours twice daily. The optimum for Kanazo and indeed for the true forests of the Delta may be described as lying between the highest low-water mark and the lowest high-water mark for the year. Where the water is comparatively fresh, growth is more vigorous and the trees reach a greater height, but where the water is more salt, the stand is thicker but the trees attain only a medium girth.

In fresh water the associates of *Heritiera* are *Amoora cuculata*, *Dysoxylum* sp., *Afzelia bijuga*, *Barringtonia* sp., *Combretum* sp., *Acanthus ilicifolius*, etc. (Type L 19 a of Stamp).

In salter water the associates are fewer in point of species and include the true mangroves (*Rhizophora mucronata* and *R. conjugata*) and *Ceriops roxburghiana*. Other trees which may be present are *Carapa moluccensis*, *C. obovata*, *Bruguiera parviflora*, *Excoecaria agallocha*, *Sonneratia griffithii*, *Cerbera odallum* and *Cynometra ramiflora*. The common ground vegetation is *Acrostichum aureum* (Type L 19 b of Stamp).

- (vi) **Low levels flooded with fresh water.** Such conditions are found along the banks of streams in the northern part of the area under consideration. The vegetation does not vary greatly from riparian vegetation elsewhere, though sometimes the more typical Delta species *Sonneratia acida* may have taken possession.
- (vii) **Low levels, flooded by salt water at all tides.** This is the home of the true mangrove swamps (Type L 21 of Stamp). In many parts of the world the mangrove swamps cover wide stretches of deltaic mud flats, but in the Irrawaddy Delta they occur only as strips along the sea face and along the banks of creeks near the sea. The characteristic mangroves are *Rhizophora mucronata*, *R. conjugata* and *Sonneratia apetala*. Others which may occur include *Bruguiera parviflora*, *Carapa obovata*, and *Sonneratia griffithii* and sometimes stretches of *S. acida*. *Nipa fruticans* is common. Another type of mangrove swamp is afforded by almost pure *Ceriops roxburghiana* with shrubs of *Aegialitis rotundifolia* and *Aegiceras majus* (khaya).

The mutual relationship of the above types of vegetation will be apparent from the diagrammatic sections, Figs. 2 and 3. In passing it may be noted that the majority of the tidal trees have pneumatophores of varying character and seeds adapted for distribution by water.

## V. INTERPRETATION OF THE AERIAL PHOTOGRAPHS.

The above account of the Irrawaddy deltaic vegetation, summarised mainly from the observations of Mr A. W. Moodie and Col. English, serves to show, amongst other things, the types of vegetation which are to be distin-

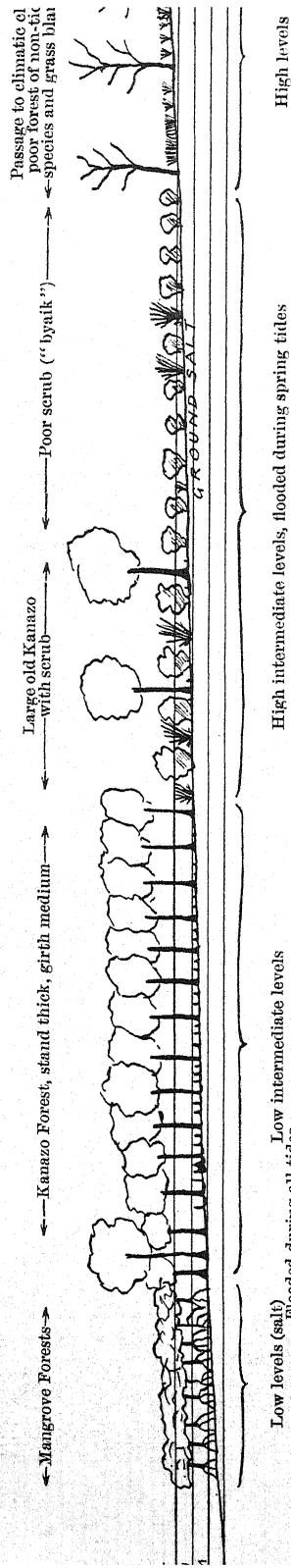


FIG. 2. Water salt or brackish.

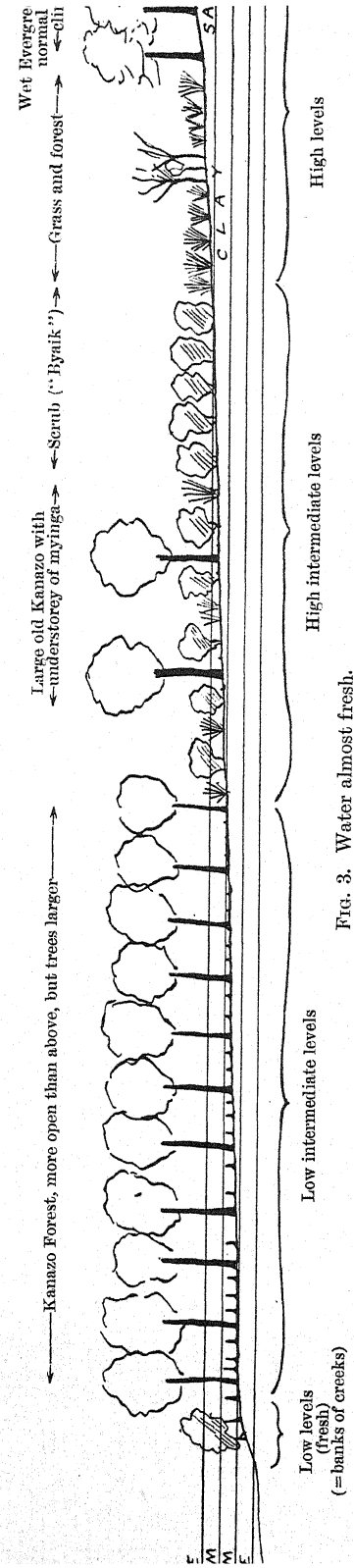


FIG. 3. Water almost fresh.

Figs. 2 and 3. Plant Succession in the Irrawaddy Delta (after A. W. Moodie)—L.D.S.

*ME* = Extreme high water mark, spring tides. *HWM* = Mean high water mark. *LWM* = Mean low water mark. *LWME* = Extreme low water mark, spring tide. The representation of trees is purely diagrammatic, though an attempt has been made to show relative sizes of Kanazo under different conditions and varying height "g", excrescences; also relative size of the scrub vegetation. The passage from a typically xerophilous vegetation to the hygrophilous vegetation which is the normal of could be noted.

guished by the observer on the ground—bearing in mind always the difficulty of penetrating into the interior of the forests. It will be seen now that some of the above types cannot be separated in the aerial photographs, whereas one or two types which stand out most clearly in the photographs do not seem to the observer on the ground worthy of separation.

During the aerial survey both Mr C. W. Scott and Mr C. R. Robbins flew over the area, making independent observations and afterwards checking their observations at certain points on the ground. The types distinguished by them may best be shown in a tabular statement, with a third column comparing their lists with those of Mr Moodie.

Distinguishable in aerial photographs		Previously distinguished on the ground by Mr A. W. Moodie	Classifica- tion of Stamp (Vegetation of Burma)
By Mr C. R. Robbins	By Mr C. W. Scott		
(a) Kanazo Forest ( <i>Heritiera fomes</i> )	(1) Kanazo Forest (unworked high forest)	(iv) and (v). Intermediate levels—Kanazo Forest	L 19 a L 19 b
(b) Kanazo Forest, heavily worked	(2) Kanazo Forest (worked high forest)		L 19 var.
(c) Kanazo Forest, with large Kambala ( <i>Sonneratia apetala</i> )	(7) "Large isolated Kambala trees standing above other growth"	Not separated	L 19 c
(d) Sandy areas with <i>Eugenia</i> sp., etc.		(i) and (ii). Inland sandy levels and sea face sandy levels	L 1 var. L 22 b
(e) Blanks and areas supporting smooth turf	(4) Grassy or sandy areas without trees or scrub growth	(iii). Clay high levels, part (grassy), also sea face	L 20 blanks
(f) Thinbaung byaik (Scrub of <i>Phoenix paludosa</i> )	(6) "Thinbaung in circular clumps in byaik"	Not separated	L 20 a
(g) Myinga byaik (Scrub of <i>Cynometra ramiflora</i> )	(3) Scrub jungle or byaik	Patches occurring in (iv)—myinga byaik	L 20 b
(h) Other byaik (of canes, etc.)		(iii). Clay high levels, part, byaik or scrub	L 20
(i) Thayaw Forest ( <i>Excoecaria agallocha</i> )	(5) Thayaw High Forest	Not separated	L 21 c
(j) Madama-Thayaw Forest ( <i>Ceriops roxburghiana</i> — <i>E. agallocha</i> )	Not separated	(vii). Low levels	L 21 b
	(8) Belts and Groups of younger Kambala trees and of Thamè trees (= m of Plate III, fig. 1)	Not separated	

#### Notes on the Table of Comparison.

(1) In general it would seem that the important types of vegetation are as easily distinguishable in the aerial photographs as in a ground survey.

(2) A few important types cannot be easily separated in the photographs. There is little or no difference between the Evergreen Dipterocarp Forests (on inland high sandy levels) and the Dune Forests (on sea face high sandy levels),

but the two can be separated by reason of the known difference of occurrence. It is, however, a matter of difficulty to separate the former from the Kanazo Forest in which it may occur as patches.

(3) There are a few types which stand out extraordinarily well in the photographs which one would not so readily separate on the ground. The two outstanding examples are the Kanazo Forest with large isolated kambala (*Sonneratia apetala*) and the byaik with little "blisters" (as they appear in the photographs) believed to be of thinbaung (*Phoenix paludosa*).

(4) Mr Robbins states that he does not "claim that the whole area, without exception, can be allotted to one or more of these types, but merely that it should be possible to recognise these types wherever they appear."

(5) Mr Scott, writing of the types which he has separated, is not very confident regarding the recognition of his type (5) Thayaw Forest, though thayaw in contrast to nearly all the common trees of the Delta Forests is deciduous and leafless in the hot season. He notes that his (6) is only a variety of (3). With regard to his type (8) the difference in the hue of the foliage of kambala and thamè enables these two to be separated by the eye in flying over the ground, but not in the photographs. He considers his (1), (2), (3) and (4) major and well-defined types, (5) needs further study, whilst (6), (7) and (8) may be considered minor types only. Further study should permit the separation of (1) into at least two qualities and also allow the separation of another major type (sandy high levels, type (d) of Robbins) which at present is not easily distinguished from Kanazo Forrest.

#### VI. MR C. R. ROBBINS' SUMMARY OF RESULTS.

Apart from flying over the Delta Forests Mr Robbins flew over some of the well-known Evergreen and Teak Forests of the Pegu Yomas—at that time of the year, February to May, leafless—and was able to incorporate his observations there. The following summary is taken from his report, with the addition of some explanatory notes and some notes by Mr C. W. Scott.

(1) The photographs were taken in the dry season—January to March. The temperature in these months gradually increases until April or May and the haziness of the atmosphere increases accordingly. The rice is harvested about November to December and a month or so later it is customary to burn off the stubble giving rise to smoke clouds. Photographs taken early in the open season when there is little haze are best for all purposes.

(2) In the interests of topographical details such as very narrow creeks, Major Lewis of the Survey of India stipulated that the photographs supplied to him for mapping should be without long shadows, i.e. should be taken between 10 a.m. and 3 p.m., more or less. Some of the best photographs from the point of view of vegetation survey (see Pls. VIII and IX) are photographs taken after 3 p.m. with long shadows which show up well the contrast between high forest and scrub. Where the forest comes right to the edge of water or

fringes a grassy blank the actual height of the trees could easily be calculated. Moreover in photographs taken in the late afternoon the edges of the various vegetation types become much clearer and individual trees of large size can be picked out by the light on their western sides and the shadows on their eastern sides. In other words photographs taken when the sun is low are best for vegetation survey or stock mapping purposes, but worst for obtaining topographical features.

(3) The different shades of green, visible to the naked eye when flying, do not show up as prominently in the photographs as might have been expected, thereby emphasising the value of aerial observation combined with photography. Alternately, comparison of the photographs with the ground as seen from the air is a great help to their interpretation.

(4) Accurate interpretation of the photographs requires a considerable preliminary comparison of some selected photograph or photographs with the corresponding areas on the ground.

(5) During the survey experiments were made with photographs taken from different heights. Pls. VIII and XII show the actual size of the photographs on the scale finally used for the survey (3.3 ins. to one mile) and taken at 10,000 ft. from the ground. At first sight it would appear that numerous advantages would accrue from photographs taken at lower elevations, say 5000 ft. Actually it was found that photographs taken at 5000 ft. added very little indeed to the details observable on a photograph taken at 10,000 ft. and enlarged to a comparable scale. Pl. IX is a photograph taken at 10,000 ft. and on the scale of 3.3 ins. to the mile enlarged twice linear, giving a scale of 6.6 ins. to the mile. It overlaps the area shown in Pl. VIII and the advantages of enlargement may be studied. Photography at lower elevation requires, of course, a much larger number of negatives, and is consequently much more expensive. 8000 to 10,000 ft. is probably the best height from which to take photographs, taking all considerations into account, including the cost.

(6) Observation from the air of leafless forests is of no value, and similarly photographs of deciduous forests taken when the trees are leafless are practically useless for the construction of a vegetation map. The leafless branches give rise to greyish areas in the photographs (see Pl. XII, fig. 2) indistinguishable from sandy or grassy blanks. The use of the stereoscope may enable one to distinguish the mass of leafless branches floating like a mist above the obscured undergrowth but that is all.

(7) A series of oblique photographs taken from heights of 1500 to 3000 ft. would have proved of great assistance in the interpretation of the vegetation and the construction of a map. This is clearly shown by Pl. XI, where the relative height of the vegetation stands out with great clearness.

(8) The aerial survey of the Delta Forests was very greatly assisted by the gregariousness of the species, but interpretation becomes difficult as soon as the species are mixed. It is doubtful whether the aerial photographic

method of stock mapping is applicable to mixed forests so typical of this and other countries. It might, however, be applied to mixed forests in which there are conspicuous consociations of certain well-marked species—such as the consociations of *Dipterocarpus tuberculatus* in the Indaing or Dry Dipterocarp Forests of Burma (Type L 9–L 10 of Stamp, *Vegetation of Burma*). In mixed forests there may also be certain species with characteristic features. Thus teak (*Tectona grandis*) when in flower should stand out clearly. Other trees are conspicuous by reason of the characteristic shapes of their crowns, or by reason of their greater height. Such trees, however, would tend to be over-emphasised in photographs of mixed forest and might create false impressions of the forest as a whole. This point is apparent to some extent from Pl. VIII, where one of the most conspicuous types of vegetation is the forest with large isolated trees of *Sonneratia apetala*. Yet on the ground, after his detailed study, Mr Moodie did not even note that some forests of *Heritiera fomes* might have a few large *Sonneratia*. Conspicuous as it is in the photographs the point is, in reality, relatively unimportant.

(9) An important practical difficulty in the aerial reconnaissance and survey of large areas of unknown forest land—such as covers enormous areas in Burma—is the absence of suitable landing places. In the Delta survey hydroplanes were used and an extension of their use to Upper Burma is made possible by the existence of broad rivers such as the Chindwin and Irrawaddy. There is then, however, a limit of some 40 or 50 miles from the river to which work may be carried with even a minimum of safety. On the other hand, if aeroplanes were used the nature of the country—forest, scrub or rice fields—is such that landing places probably do not exist.

(10) In such cases, however, observation from the air might prove a valuable means of preliminary inspection. In a country like Burma, where large areas are virtually unexplored so far as their timber resources are concerned, a few hours' flight might prove of great value.

(11) The difficulties of aerial survey in forested hilly regions have been discussed here in view of the likelihood of aerial survey in other parts of the world where it is probable that a vegetation survey might be extremely difficult. In the flat Delta forest, as Pls. VII, VIII, IX and X show, much of the information is gained from light and shade effects, the sole factor to be considered being the size and shape of the trees themselves and the thickness of the growth. In hilly regions, however, the major light and shade effects are the result of inequalities in the ground.

(12) One of the great drawbacks to an aerial vegetation survey, in forested regions, is the lack of information concerning undergrowth. In high forest a lower storey may be separable but at best the nature of the undergrowth must remain largely a matter of guesswork.

(13) The Delta Survey has brought out the advantages of glossy over matt paper. The glossy paper helps to show up detail in poor photographs like that shown on Pl. XII, fig. 1.

(14) The use of the stereoscope holds out considerable possibilities. It can best be applied to the areas of overlap of two adjacent photographs, but it is not without results when used with two prints of the same photograph. The main use of the stereoscope is to bring out differences in height of the trees which are not visible on a photograph to the naked eye or with an ordinary lens. The differences in height as seen with a stereoscope are comparative only as the apparent difference increases with the distance flown between the exposures of the two photographs giving the overlap. Scattered high forest over or among lower growth comes out very clearly as, for example, in the areas that have been heavily worked. A stereoscopic inspection is also useful for distinguishing the main crop from a subsidiary understorey. Thus an area which appears to be covered with a fairly dense even forest may be discovered to be a moderately open high forest over an understorey. This will enable forests to be allotted to quality classes. The application of the stereoscope to the separation of leafless deciduous forest from grassy blanks or low undergrowth has been noted above. Another possible use of the stereoscope is the counting of trees on an area as the individual trees stand up much more clearly from the undergrowth.

#### VII. EXPLANATION OF THE PLATES.

**Pl. VII.** A typical photograph of the Delta Forests, enlarged  $\frac{1}{2}$  times the original negative, giving a scale of 5.7 ins. to one mile. Locality near the main Irrawaddy distributary, about 12-13 miles from the sea, Kadonkani Forest Reserve. Time of exposure: early afternoon, giving small shadows on the eastern sides of the trees. Points to be noted: (1) the narrow creeks which would be obscured were the shadows longer, (2) the conspicuous large trees of *Sonneratia apetala* with light green foliage in forest of *Heritiera fomes* (on the west), (3) the interior patches of scrub or byaik with "blisters" (see p. 272) above the level for *Heritiera*, (4) the even *Heritiera* forest in the north-east. This plate is reproduced from Pl. I of the *Vegetation of Burma* (University of Rangoon Research Monograph No. 1, 1924).

**Pl. VIII.** Reproduction of photograph of the actual size and scale used in the survey, viz. 3.3 ins. to one mile. Locality: near the main Irrawaddy distributary, about 12 miles from the sea, Kadonkani Forest Reserve, a short distance to the south of Pl. VII. Time of exposure: late afternoon, giving long shadows. Points to be noted: (1) the advantage of long shadows in showing up the relative height of the vegetation, (2) the mode of occurrence of the true mangrove forests and allied types fringing the banks of creeks. For further explanation see Key.

**Pl. IX.** The area immediately to the south of that shown in Pl. VIII, fig. 1. There is an overlap of about 40 per cent. and this photograph illustrates the effect of enlarging the originals to twice the scale, giving a scale of 6.6 ins. to the mile. A careful comparison of the two photographs should be made for



some difference of opinion may exist as to the advantages or otherwise of enlargement) just as with photographs taken at 5000 ft. there is perhaps a tendency for greater detail to confuse matters. On the islands (to the west) and in the north-east is Kanazo Forest (*Heritiera fomes*) with scattered *Samanea* (*Sonneratia apiculata*). In the south-east is Kanazo forest interrupted by patches of byaik or scrub, consisting mainly of *Cynometra ramiflora* with thamé (*Albizia officinalis*).

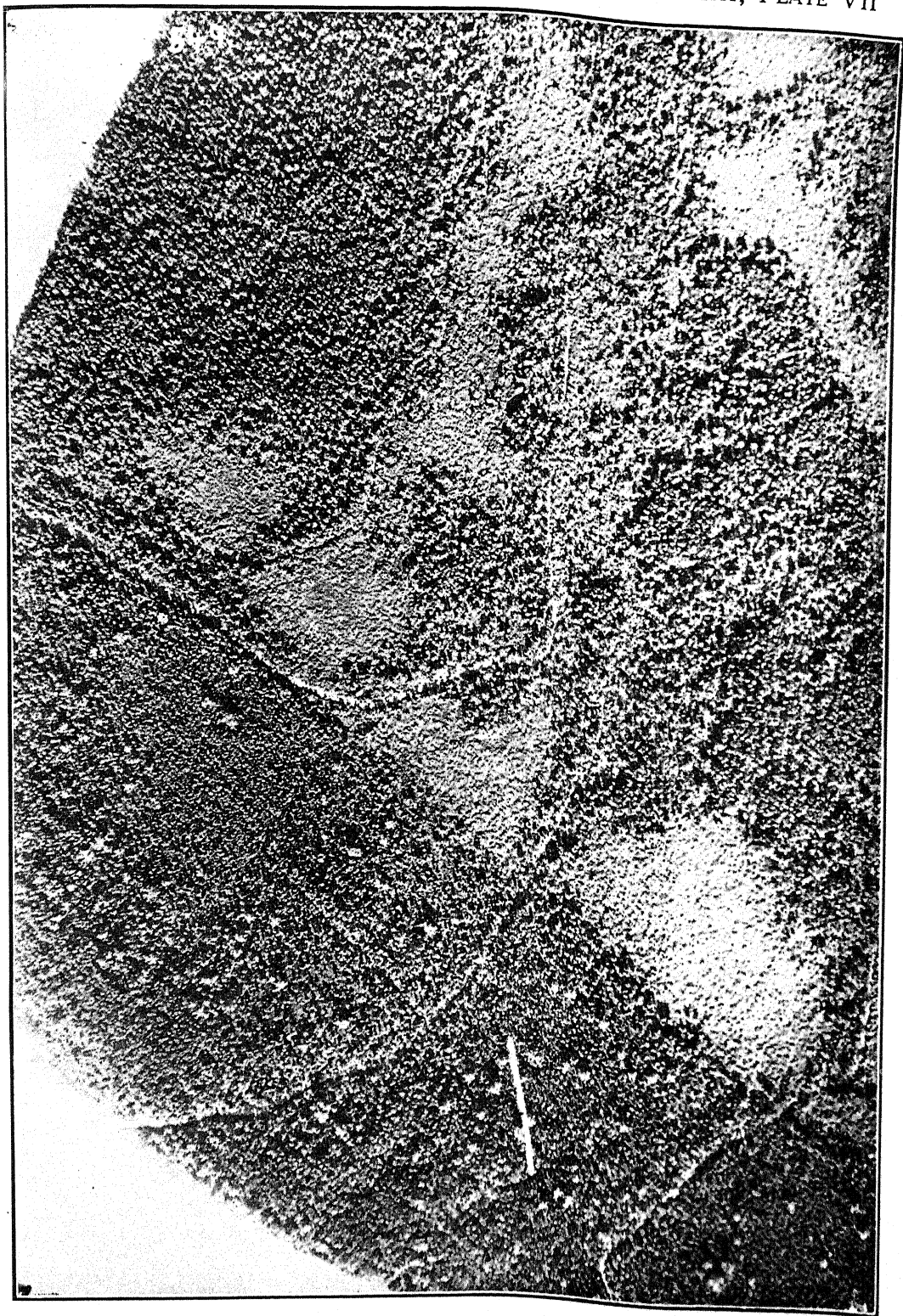
Locality: Kalyank Forest Reserve, south-west of Moulmein. Time of exposure: late forenoon. Photograph enlarged to the scale of 66 ms to one mile. Although the time of exposure can generally be gauged by a study of the shadows, confusion is possible and this photograph should be compared with the other two photographs of Pls. VII and IX. This photograph is typical of areas where the vegetation is more varied and the eastern half illustrates the difficulties presented by regions where forest and scrub appear to be much intermingled. The ground observer would probably be able to separate several types of scrub or byaik.

Pl. XII. An oblique aerial photograph taken from a height of about 1500 ft. It illustrates, without any emphasis being necessary, the great value of oblique aerial photographs as an adjunct in an aerial vegetation survey. The types present are *Heritiera fomes* (Kanazo) Forest; scrub or byaik and, in the middle foreground "blanks" probably grass covered. Locality: east of the Kadonkani Forest Reserve. This plate is reproduced from Pl. XXII of the *Vegetation of Burma*.

Pl. XII, fig. 1. This photograph is especially selected as being much below average quality owing to mist and haze. The original photograph was much improved by the use of glossy paper. It is possible to distinguish the darker areas of *Heritiera* forest and the lighter, smoother areas of *Eragrostis*, *Cerios*, *Cynometra* etc. Darker areas along stream banks may be of different species.

Fig. 2. Locality: Lelyank Reserve, including a considerable area of inland high sandy levels covered with moist mixed deciduous forest. The areas of tidal forest show very dark, the leafless deciduous forest light. Part of the area covered by the latter has been cultivated and afterwards allowed to return to forest. The boundaries of such areas ("poszos") appear as clear-cut lines. Fig. 2 is reproduced from Pl. XXIII, fig. 2, of the *Vegetation of Burma*.

For plates illustrating some of the vegetation types here described reference should be made to the writer's *Vegetation of Burma* (University of Rangoon Research Monograph No. 1, 1924).



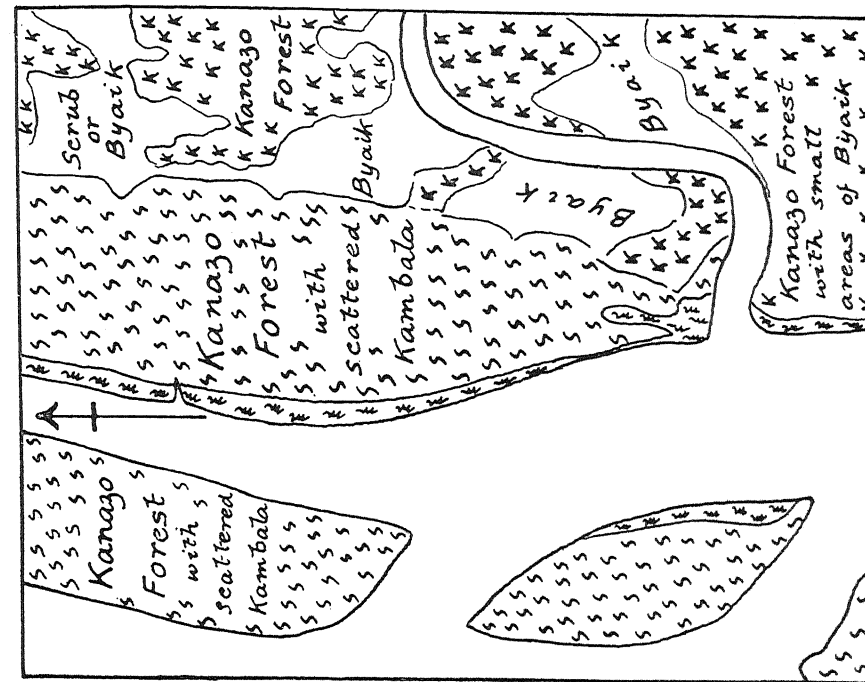
Part of Kadonkani Forest Reserve.

STAMP—AERIAL SURVEY OF IRRAWADDY DELTA





STAMP—AERIAL SURVEY OF IRRAWADDY DELTA



Part of Kadonkani Reserve

NOTE: The species composing the fringe forests (*m*) in this particular case are *Sonneratia apetala* and *Avicennia officinalis*, but elsewhere strips of true mangrove swamp occur in similar positions.



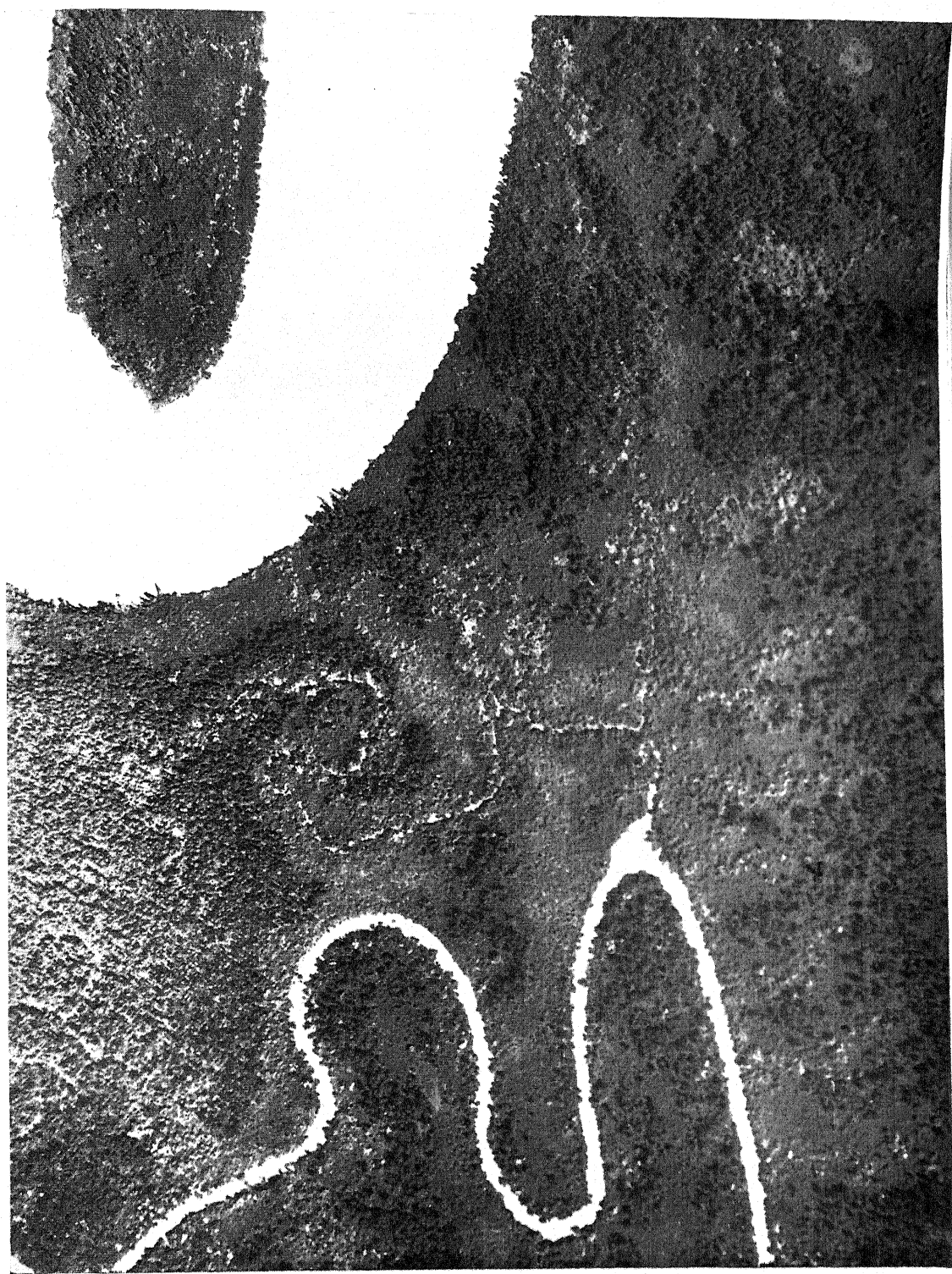


Part of Kadonkani Reserve.

STAMP—AERIAL SURVEY OF IRRAWADDY DELTA





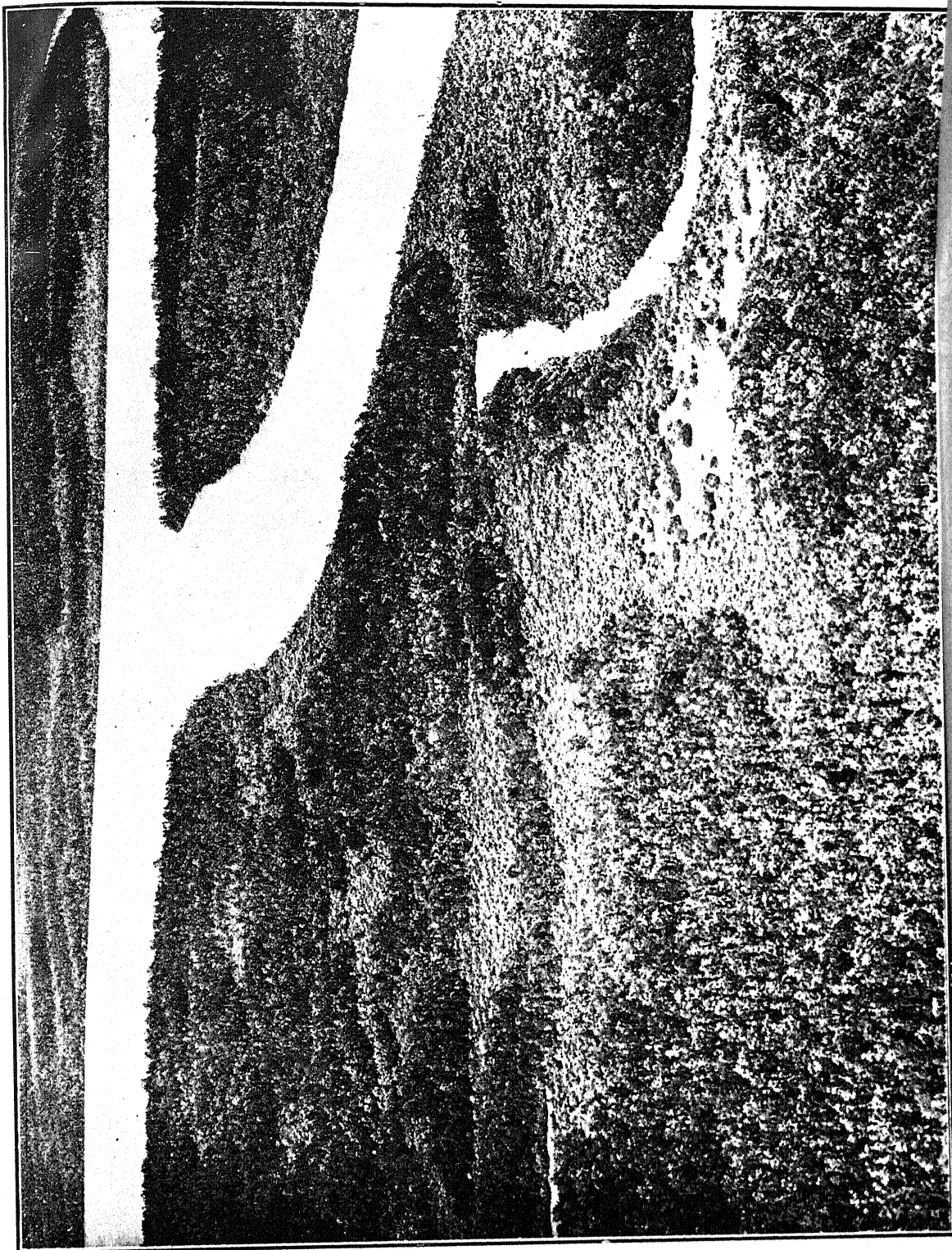


Part of Kalayaik Reserve.

STAMP—AERIAL SURVEY OF IRRAWADDY DELTA







STAMP—AERIAL SURVEY OF IRRAWADDY DELTA





FIG. 1. Land obscured by mist and haze.



FIG. 2. Part of the Lebyauk Reserve.

STAMP—AERIAL SURVEY OF IRRAWADDY DELTA





# THE TECHNIQUE OF RESEARCH ON MARINE PHYTOPLANKTON

By BLODWEN LLOYD.

(With three Figures in the Text.)

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DURING the period from October, 1922, to March, 1924, a preliminary investigation of the phytoplankton of Cardigan Bay was undertaken<sup>1</sup>. A study of the plankton flora, as indeed of nearly all minute living forms, necessitates special methods of capture and preservation. In this paper the technique adopted will be considered.

*Historical.* The "Challenger" Expedition of 1872 gave great impetus to the development of a definite science of oceanography; this and subsequent expeditions resulted in an increased realisation that the minute free-floating plant forms were highly significant in the general economy of the sea. The term "plankton" was first applied to such "wandering" forms by Hensen in 1887. From his time onwards, greater attention was paid to more accurate methods of capture and estimation, and by the end of the last century, there had arisen a distinctive school of plankton workers, the Kiel planktonologists. Since that time these and other workers have elaborated many and varied devices for the capture of plankton under known or calculable conditions, and for the subsequent accurate estimation of the catch.

### 1. COLLECTING.

Within the last fifty years a variety of methods of plankton collecting have been devised, each with its strong advocates. With regard to the present status of these methods, W. E. Allen (1) holds that "there is little hope of innovation...the best prospects seem to lie in the development and continuance of methods, activities and plans already known and tried."

(a) *The horizontal tow-net.* For accurate intensive work, many elaborate types of tow-nets have been evolved, but the open conical tow-net used for "Challenger" tows has yet maintained a place. Its usefulness for general

<sup>1</sup> The results were published in this JOURNAL, 13, 1925, pp. 92-120.

plankton collecting is due largely to the comparative ease with which it is manipulated.

I am indebted to Miss M. Knight, D.Sc., Liverpool, and to Dr J. Johnstone, Liverpool, for much helpful advice as to the making of tow-nets and as to general methods. The nets used were constructed after the usual pattern, of bolting silk (Müllergaze) No. 20, with a pentagonal mesh of 172 to the linear inch. Although able to withstand a greater strain than silk of ordinary weave, the threads of the bolting silk became swollen and distorted with constant use, so that the filtration capacity of the mesh decreased considerably after a time (Fig. 1).

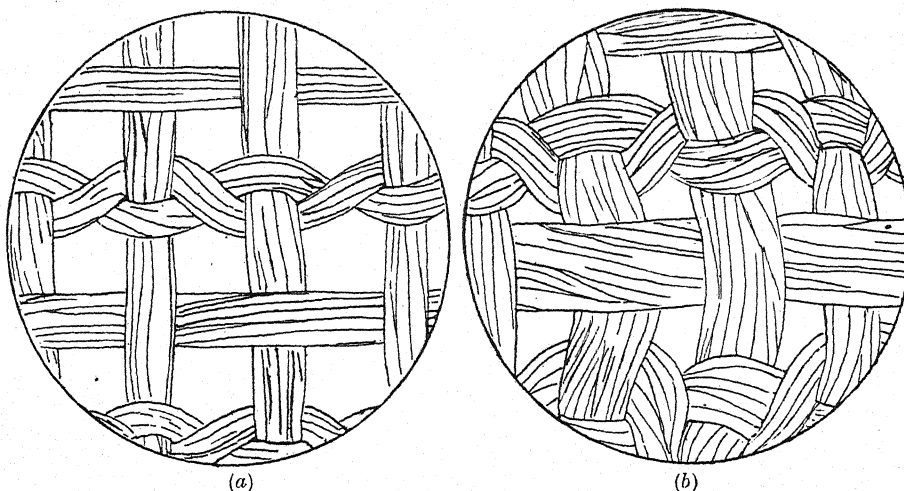


FIG. 1. Bolting silk (Müllergaze) No. 20. (a) New; (b) after six months' use.  $\times 60$ .

A conical bag of the silk was attached by a strengthening headpiece of strong fustian to a copper ring. Three headropes of mackerel line attached the net to a rope of sufficient length to keep clear of the wake of the boat when in motion. The two small nets used for comparative purposes were 25 cm. in diameter at the mouthpiece, with a total length of 68 cm.; two other and larger nets had a diameter of 30 cm. at the mouthpiece, and were 100 cm. in length. The conditions of usage are considered below.

(b) *The Planktonröhre* was found useful on certain occasions. Apstein's model was used, a hollow brass cylinder 25 cm. long by 3.5 in diameter, fitted at the forward end with a mouthpiece in the form of a truncated cone 1 cm. in diameter, and at the other with a detachable filtering disc of bolting silk. The narrow mouthpiece prevents excessive inflow of water. After towing the tube through the water, it could be hauled on board, the silk unfastened, and the captured organisms washed out of it. The outstanding advantage of this apparatus is that it can be worked at a greater speed, for example, from fast motor-boats going at a speed which would tear the silk of the tow-net; its

principal disadvantage lay in the relatively small amount of water filtered, with a corresponding diminution in the volume of the catch thus obtained.

It was suggested to me<sup>1</sup> that the modifying of Apstein's type, namely, by inverting the mouthpiece, would result in an increased entry of water without a disproportionately greater strain on the silk at the rear (Fig. 2). By this means a somewhat larger catch was obtainable, while the increased pressure caused by the greater inflow of water did not visibly damage the micro-organisms more than in the first case. But even here the quantities obtained were always extremely small, a 20-minutes' towing during the March phase of increasing phytoplankton giving only 0.1 c.c. wet volume.

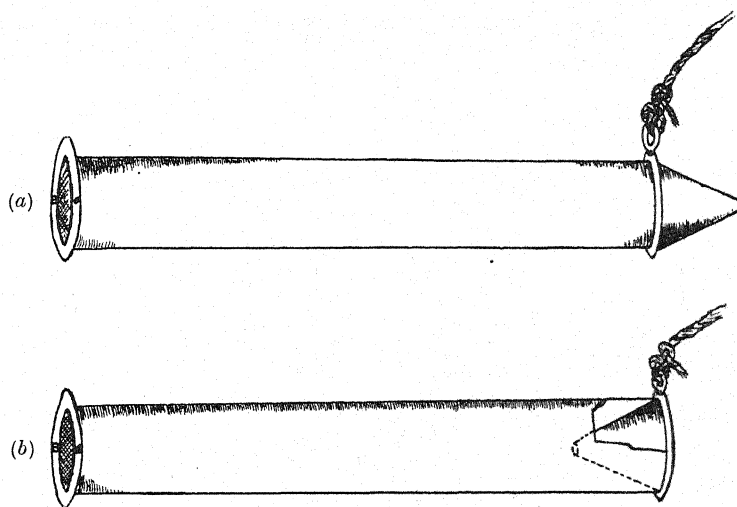


FIG. 2. Planktonröhre: (a) Apstein's type, with everted mouthpiece; (b) with inverted mouthpiece.  $\times \frac{1}{2}$ .

Another modification found to be useful at times was the interspersing of coarser filtering meshes at the forward end of the tube; the catch could thus be sorted roughly into sizes as made. For instance, a disc of coarse muslin just below the mouthpiece retained the larger zooplankton—copepods, and a variety of larval stages, while at the posterior end were found the diatoms, peridinians and small protozoa. This device was found to be particularly useful when there was a "mixed" catch of phytoplankton and zooplankton.

(c) For the study of those very small forms which constitute the nanoplankton, the *centrifuge* was used in the summer months; by this method the micro-organisms missed by even the fine-meshed net could be sedimented. From the spring of 1923 onwards, when tow-nettings were made, surface water-samples were usually taken and centrifuged on landing.

Two types of centrifuge were employed, a two-speed hand model working

<sup>1</sup> For this, and many other helpful suggestions, I am indebted to my father, Mr W. Lloyd, of Aberdare.

at about 1600 revolutions per minute, on the fast gear, when fully loaded, also a water-turbine model working at a slower rate. Both carried four tubes; for general purposes, the ordinary conical glass tube of 15 c.c. capacity was used, but where the quantity of plankton was very small, tubes after Lohmann's pattern, with a prolonged narrow apex, and a capacity of 10 c.c., were employed. Following the method described by Dr Lebour (9), for counting work, the water is centrifuged, and the supernatant liquid poured off and recentrifuged; finally the total sediments are pipetted on to a cavity slide for estimation. In this way the contents of 60 c.c. of sea-water could be collected into about 0.1 c.c. for examination and counting. The work done with regard to the centrifuging of nannoplankton was more in the nature of obtaining supplementary records to those of the tow-net catches, rather than a systematic study of these small forms.

(d) *Filtering methods.* The method advocated by W. E. Allen (1) of filtering a known volume of water by means of a very small net was applied more particularly to a study of the littoral waters and rock pools, where the large tow-net was naturally of little use. A net of the same pattern as the horizontal tow-net but with a diameter of 8.5 cm. and a length of 12.0 cm., was used. For the shore flora this was found to yield very interesting results.

#### *Methods of Tow-netting.*

The large horizontal tow-nets were found to be the most convenient for general purposes. They have been strongly denounced as inadequate, especially for comparative statistical work: "Evidently then tow-net catches give no trustworthy indication of the relative amounts of phytoplankton in two different locations or in the same location at two different times, although they may have a high suggestive value" (*l.c.*). Nevertheless, in that they filter a much larger volume than can be conveniently handled by other methods, the possible range of error is less significant. For this reason therefore, notwithstanding its acknowledged disadvantages, the tow-net was used very largely in the course of the work done, and supplemented where desirable by other methods.

For regular sampling, the nets were towed along a given course for 15 minutes from a small rowing boat. The nature of the course varied somewhat with state of the tide and wind, but whenever practicable, the catch was made  $1\frac{1}{2}$  to 2 miles from shore. It was originally intended to make bi-weekly tow-nettings, but this was found to be impracticable. During 1923 the weather was particularly unfavourable; the report of the Superintendent of the Lancashire Sea Fisheries Board stated that such wild and unfavourable conditions for trawlers had not been experienced in the past 19 years. Even in the month of July it was found possible to make tow-nettings on two dates only.



The catch once made, the next step was to turn it out of the net with as little loss of contained organisms as possible. The flow of water through the net tended to carry most of the captured organisms to the apex, but some, especially the more spiny forms, became entangled in the upper meshes of the filtering area. On larger boats where the net can be hauled vertically from the sea, the captured organisms can be impelled downwards by the impact of water from a bucket or a hose, on to the outside of the net. From the small boat it was endeavoured to achieve the same purpose by raising the mouth-piece above water-level, and allowing the net to trail while the boat was still in motion; those forms entangled in the sides of the net thus tended to be washed down to the apex.

It should be noted that even here where a catch is made under known conditions of tide, speed of boat, filtration capacity of net, etc., it is debatable as to how far the haul is representative of the actual plankton in the sea at the time. Were the plankton widely distributed in a uniform manner, the catch might be considered as typical within a reasonable margin of error. However, the bulk of the evidence gathered by planktonologists seems to favour the view that the component associations of the plankton exist in shoals or "streaks," called "zoorema" by Haeckel<sup>1</sup>; but it is a moot point as to whether these postulated streaks exist as a definite ecological unit, as in the case of migratory fishes, or as a simple fortuitous grouping resultant upon the movements of ocean currents.

## 2. FIXING AND PRESERVING.

When living material was required the catch was turned out into plenty of sea-water for transit ashore; these conditions were widely different naturally from the normal surroundings of the organism, and the effect of such close confinement was found to vary both with the species and with the particular catch made. Whereas some forms, for example the diatom *Coscinodiscus radiatus*, lived and even multiplied when kept in a jar in the laboratory for some 6 to 10 days, the peridinian *Ceratium* was only occasionally brought to land in a normal condition. A notable exception was the catch of February 12th, 1923, made in a heavy shower of rain with a high sea running. *Ceratium fusus* was abundant in this haul, and on landing, the rich brown fusiform cells were observed to be in vigorous motion. The extreme sensitiveness of this genus to unfavourable conditions manifested itself in a somewhat remarkable reaction. Whereas in changed circumstances the diatoms became vacuolated, with ultimate collapse of the cell-contents, the plasma of the Ceratia was often observed to have exuded through the ventral plate, and frequently remained as a brown sphere attached to the empty theca. This curious circumstance will be considered later.

This variability on the part of the organisms comprising the catch made

<sup>1</sup> Haeckel. *Planktonstudien*, Jena, 1890.

it advisable that the haul should be fixed while on board, except where the living forms were specially desired. For this a 5 per cent. solution of commercial formalin in sea-water was largely used. Its especial merit lay in its swift hardening action, while at the same time it preserved the coloured elements in the plasma and gave no inconvenient precipitates with the sea-water. Its acid reaction, due to the formation of formic acid in the solution in the presence of light, causes it to dissolve the tests of such calcareous micro-organisms as the Coccolithophoridae. These, however, are not of frequent occurrence in offshore waters. If necessary, the solution can be neutralised with magnesium carbonate, and then stored in a stock bottle of dark glass. Almost all the "regular" catches were fixed with formalin; 90 per cent. alcohol was used occasionally. The precipitate it gave with the sea-water could be removed by decanting the latter and replacing with distilled water. Formalin-spirit (95 c.c. of 70 per cent. alcohol; 5 c.c. of commercial formalin) was also used.

For detailed work, special fixing agents were taken on board. In using Flemming's strong solution, Gran's method was adopted: a small portion of the catch was washed into sea-water, and Flemming's solution added in the proportion of 1 : 25. Other fixing agents used were 1 per cent. chrom-acetic in sea-water, and Bouin's fixing fluid (picric acid 75 parts, commercial formalin 25, glacial acetic 5).

### 3. MICROTECHNIQUE.

The beauty and symmetry of the siliceous tests of diatoms are largely responsible for their popularity in microscopy. Most plankton diatoms are only feebly silicified, and are therefore not suited for preparations necessitating treatment with strong acids; moreover, when it was required to stain the cell-contents, it was found difficult to establish an order of treatment that would serve all species equally well.

*Mounting diatom frustules.* Where only the empty exoskeleton was required, there was naturally no necessity for preliminary fixing. In the case of the more feebly silicified forms, clearing with potassium hydrate or eau-de-Javelle dissolved the cell-contents, though the time taken varied from a few hours to a few days.

For the very siliceous forms, chiefly littoral species, the special method described by Van Heurck (12) was found to give good results. The organic contents were first removed by digesting in cold hydrochloric acid, followed if necessary by boiling in concentrated nitric acid. The diatoms were then washed thoroughly with distilled water; at this stage they could be decanted off from any foreign quartz particles present.

Dehydration prior to mounting was accomplished by passing up through the alcohol series:

10...20...30.....90...95 per cent....absolute.

This work was carried on in small embedding bottles with a cubic capacity of 5 c.c.; about 10 minutes for each grade, with longer periods in 95 per cent. and absolute alcohol, sufficed.

It was found impracticable to dehydrate by drying in air, owing to the fact that some forms were so bulky that the imbibing solution used prior to the mountant often entered the diatom so quickly as to enclose an air bubble.

Mounting from xylol into Canada balsam gave only a poor resolution of fine detail in the cell-walls, owing to the very similar refractive indices of the balsam and the siliceous walls. For better resolution of the striae and alveoles in the cell-wall, the special method of mounting in *styrax* described by Van Heurck (12) was adopted. *Styrax* has a considerably higher refractive index than Canada balsam, and, being of a similar resinous nature, is equally permanent. A thick solution in benzol was employed.

A drop of the diatomiferous absolute alcohol is placed on the cover-glass, or on the slide directly; a drop of benzol is first added, and followed by a drop of the mounting medium. The preparation is usually found to become milky white at this stage (Van Heurck states that this does not occur with the *styrax* dissolved in chloroform). The slide is then placed under a bell-jar for 1 to 2 days, during which time the milky appearance vanishes. A cover-glass or slide, as the case requires, is then passed through the flame of a spirit lamp, and mounted over the preparation, which hardens very soon, and requires no sealing.

Many diatoms of the littoral epiflora can be treated as described above, but the genera *Grammatophora*, *Amphora* and *Cocconeis* were found to be only slightly silicified and therefore unsuitable for such treatment.

*Plasma staining.* The prime difficulty in the technique of staining phytoplankton forms is that of carrying these small unicellular forms through all the processes without loss or injury.

The prolonged washing necessary after some fixing agents, especially those containing chromic acid, was accomplished by placing the diatoms in a small bottle 38 mm. high, and by securing with a rubber band a small disc of bolting silk over the mouth; a jet of water could then with safety be allowed to play on the silk for as long as was needed. Staining, and all the processes up to the last stage before mounting were carried on in tubes—centrifuge tubes were found to be extremely satisfactory, for where treatment for a short space of time was necessary, the organisms could be centrifuged immediately and the reagent decanted.

The difficulty in staining was that in a mixed collection, as most plankton catches were, there was naturally great variation in the degree of staining; in fact, it was found impossible to obtain a uniform depth of stain in the same preparation. A double stain with safranin as selective stain and orange G as a plasma stain was found to react with moderate brilliance; the former was allowed to act for 3 days, and the latter for 8 hours. It was found im-

possible to get Flemming's triple combination to act, owing to the difficulty of retaining the gentian violet. This was probably due to the purely mechanical difficulty of minimising the time taken over changing the absolute alcohol and the xylol in the centrifuge tubes, a space of time longer than is required for the same process on a slide. The method described by Zimmermann<sup>1</sup>, of increasing the brilliance of aniline dyes by mordanting with formaldehyde, was employed.

As in the case of the gentian violet, a similar difficulty was experienced with Haidenhain's iron-alum haematoxylin; here there was the difficulty of destaining to the right degree. The following schedule was found to be satisfactory:

Iron-alum,  $1\frac{1}{2}$  hours,  
Wash with water, 5 minutes,  
 $\frac{1}{2}$  per cent. haematoxylin, 12 hours,  
Wash with water, 5 minutes,  
Iron-alum, 10 to 15 minutes,  
Wash, 1 hour.

Lest the dye-extraction in the last stage should go too far, a control slide was watched under the microscope while the mordant was acting on the bulk of the material in the centrifuge tube.

For simultaneous fixing and staining acetic carmine was found to be useful, particularly with some species which did not react well with other fixing agents. The curious diatom *Streptotheca thamensis* was found to be fixed with little shrinkage when treated for 6 to 12 hours with acetic carmine. After staining, mounts were made in Canada balsam or glycerine jelly.

*Sectioning.* An attempt was made to study nuclear division in the larger diatom forms, but, mounted whole, they were so bulky as to render examination with the oil-immersion lens a matter of some difficulty. These were therefore embedded for cutting, by embedding in paraffin wax. Hand sections of the paraffin blocks, with the contained diatoms, gave a rough sectioning which enabled the nucleus to be seen more clearly. Serial sections were also cut with the microtome, but the masses of diatoms tended to make the ribbon brittle; further, even with the use of a specially hardened microtome knife, the splintering of the walls of the frustules tended to tear away from, and thus distort the cell-contents.

#### 4. EXAMINATION AND ESTIMATION.

(a) *Volumetric.* When the plankton catch was brought into the laboratory, it was first subjected to preliminary observation of its general characteristics, the predominant organisms, and other striking features. The material was then placed in tall tubes 10 mm. in diameter, and allowed to sediment, the time taken varying with the nature of the catch. A surface catch consisting

<sup>1</sup> Zimmermann. *Botanical Microtechnique*, London, 1896.

mainly of the diatom *Rhizosolenia*, takes several days for complete sedimentation, while on the other hand a haul of copepods will settle in about 30 minutes. In cases such as the former, the organisms were first collected by centrifuging, and then poured into the narrow tubes for estimation. The catch was allowed to settle till the liquid was perfectly clear, and the level reached by the organisms noted by a mark on the tube. The plankton was then removed, and the volume it had occupied was replaced with a measured volume of water.

This volumetric method, while in itself no conclusive guide to variation in the plankton, gives results of great interest when correlated with other methods of estimation.

(b) *Biometric*. The catch was shaken up into 50 c.c. of water, and while the organisms were still suspended, a small quantity, usually 0.2 c.c., was withdrawn by means of a fine pipette on to a cavity slide. The frequency or rarity of the species present was then determined; the contents were noted for that portion of the catch on the slide, and were taken as being representative within certain limits of the total catch. A table was then constructed for the plankton flora according to the following frequency-scale:

cc.	Very common.
c.	Common.
f.	Frequent.
r.	Rare.
rr.	Very rare.

It was held that the method of estimation by counting entailed a degree of accurate work not compatible with the wide range of unknown conditions, such as rate of hauling, under which the horizontal haul was made, and it was therefore not employed for general work. "Some observers count 1 c.c. at a certain dilution. Not only does this method introduce the error of excessive fatigue into the work, but it also uses an amount of time which prohibits the examination of any large number of samples. Its questionable gain in accuracy is not at all commensurate with its drain on time and energy" (1).

Dakin, on the other hand, holds that "quite false results are obtained by the method of estimation without counting" (5). In support of this he cites a pair of plankton catches, where an organism *A* might be numerically the same in both cases, but where in the second case, the predominance of another form *B* might overshadow it; on a basis of frequency-estimation *A* might be recorded in the first catch as cc. and in the second as + or even r. It is true that the statistical method gives absolute data, and that the frequency-table gives only relative values, and, furthermore brings in the personal element as another possible source of error. Now in both the above-quoted cases statistical records for the species *A* would be the same; but, other things being equal,

the salient feature to a plankton consumer in search of its food, is, not the equal abundance of *A* on both occasions, but rather the greater abundance of the species *B* at the time of the second catch. It would seem therefore that the comparative method of estimation conveys a better conception of the phytoplankton as ocean "pasturage" than do figures alone. At all events, as in the case of terrestrial plant ecology, the present-day balance of opinion seems to incline away from the accurate counting methods introduced by the Kiel school of planktonologists.

## 5. CULTIVATION.

It was thought that if phytoplankton organisms could be induced to grow in the laboratory, such a supply of living material would be useful for cytological work. Accordingly, though time would not permit of extensive cultural experiments, some attempt was made to obtain mixed growths. Allen and Nelson's method (2) was adopted.

A litre of ordinary sea-water was sterilised by heating almost to boiling point for 20 minutes; 2 c.c. of Allen's nutrient solution *A* and 1 c.c. of solution *B* were added, and the whole shaken up. The resulting precipitate was removed and the mixture inoculated with a drop of sea-water containing living plankton. The whole was then distributed into petri dishes and small conical flasks. The first series was planted on January 23rd, 1923, but met with little success. Within three weeks all the plankton forms had died off, and there was no evidence that multiplication had taken place. Series similar to the above were started on April 4th, February 10th and May 23rd, but met with the same fate. There was, however, a vigorous bottom growth of small benthic diatoms chiefly, with often a green confervoid growth on the sides of the vessel.

It was thought that possibly the materials used for the nutrient solutions were not chemically pure. Accordingly, on June 1st some natural untreated sea-water was inoculated with living plankton. Most of the forms, the zooplankton especially, died off soon. A week later it was observed that *Chaetoceras* spp., *Ditylimum brightwelli*, *Coscinodiscus radiatus* and *Biddulphia mobiliensis* were quite healthy and dividing vigorously. But the *Ditylimum* first began to look unhealthy, forming highly refractive fatty globules terminally; within another 18 days all the plankton forms were dead. Finally, it was found that by inoculating a 2-litre flask of ordinary sea-water with a small quantity of living plankton, the same could be kept alive for a space of time varying from a few days to a month.

Although the keeping of plankton alive in the laboratory was a matter of uncertainty, some interesting light was thrown on the succession of protista under cultural conditions. Allen notes the extreme difficulty of keeping a plankton culture pure; in the experiments cited above, no especial care, beyond the preliminary sterilisation of the sea-water, was taken to exclude

extraneous living forms. It was noted that these intruders seemed to follow in a definite order in point of time:

Plankton forms.  
Saprophytic protista.  
Benthic forms.

Of the plankton forms, those that persisted the greatest length of time were *Skeletonema* and *Asterionella*. The latter became unusually pale in colour, and tended to divide to form a straight rather than the normal star-shaped filament. *Skeletonema* too became much deformed and indeed scarcely recognisable. The chromatophores degenerate, the frustules acquire a blue tinge and become curiously contorted and often abnormally lengthened or shortened; the nuclei fragment, the spines break up, and finally we have the strangest extreme forms (Fig. 3 c).

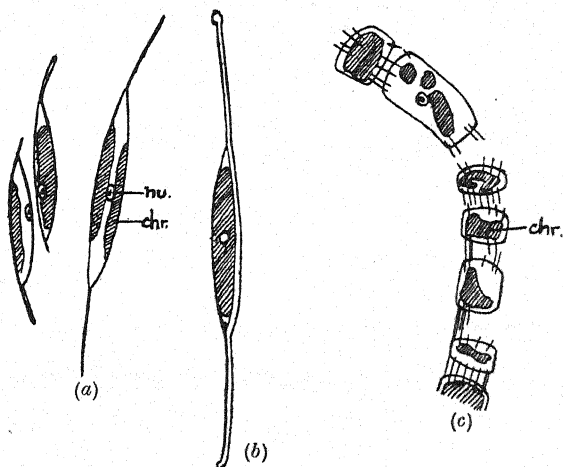


FIG. 3. (a) *Nitzschia closterium*: non-motile form; (b) *Nitzschia closterium*: motile form; (c) *Skeletonema costatum*, abnormal culture form.  $\times 335$ .

The ubiquitous *Nitzschia closterium* thrive exceedingly well, and survived all other forms by many months. The short non-motile form was the first to appear, followed later by the more robust motile form. Both forms were distinctive, and no intermediate stages were observed. Dr Lebour (9) states that the latter is a developmental stage of the former. It may therefore be suggested here that *N. closterium*, like some animal forms, spends its early days in the non-motile plankton-phase, but at a later date in its life-history assumes a motile benthic habit (Fig. 3 a and b). Certain data from the tow-net catches seem to support this.

As the plankton diatoms died off in the culture dishes, there arose a swarm of small saprophytic forms, for the most part of simple structure. These clustered round the empty frustules of diatoms, and were particularly abundant

in the vicinity of dead copepods. *Peridinium* spp. were occasionally found alive under such conditions. Small protozoan forms developed in great numbers, while of the protophyta *Oxyrrhis marina* and various Cryptomonad forms were most abundant.

These forms, with the exception of *N. closterium*, usually died off in 8 or 9 weeks at most, apparently for lack of suitable nourishment. Following close upon them we have the third phase, that of the benthic autotrophic diatoms, chiefly *N. closterium*, *Schizonema Grevillei*, *Pleurosigma* spp. and *Naviculæ minutissimæ*. These persisted for weeks or even two or three months, but the conditions that made for their success, as compared with the difficulty of keeping plankton forms alive, were not fully investigated.

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# TWO RELICT UPLAND OAK WOODS IN CUMBERLAND

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*(With Plates XIII and XIV and three Figures in the Text.)*

## INTRODUCTION.

EXAMPLES of woodland which one may reasonably consider to be primitive are undoubtedly of rare occurrence in this country (6); consequently, such examples, when encountered, are of particular interest to the ecologist.

The two small oak woods which are here described, although they have certainly not, in the course of their history, been entirely free from human interference, can probably lay claim to be as nearly virgin in nature as any others in Great Britain. These woods, which are shown in Fig. 1, are locally



FIG. 1. View looking across the Newlands Valley, showing the Keskadale Oaks on the hillside to the left, and the Birkrigg Oaks on the right. (Drawing made from a photograph.)

known as the Birkrigg Oaks and the Keskadale Oaks. They are respectively situated on the southern slopes of Causey Pike, and Ard Craggs, two parallel and adjacent mountain ridges lying between Derwentwater and Crummock Water in Cumberland, some five miles to the south-west of Keswick.

The above drawing of the two woods was made from a photograph taken from a point on the opposite side of the Newlands Valley and approximately

two miles due west of the Keskadale Oaks (seen on the hillside to the left). The Birkrigg Oaks, seen on the right of the drawing, are about three-quarters of a mile to the south-west of the Keskadale Oaks.

As will be gathered from an examination of Fig. 1, both woods occupy very similar positions as regards slope of ground and aspect. They are both, as far as it has been possible to ascertain, practically pure associations of *Quercus sessiliflora* (no *Q. robur* having been observed), and they both lie between the 1000 ft. and 1500 ft. contours, i.e. above the usual limit of *Quercetum sessiliflorae* in this country (8). Both grow on the same type of shallow, stony, argillaceous soil which in many places becomes moving scree. This soil was found to have in both cases a decidedly acid reaction (tests with the B.D.H. "Universal Indicator" showed a pH value of approximately 5) and is formed by the weathering of the shaly rock of which the ridges are composed, and which belongs to the Skiddaw series of the Lower Silurian Formation.

The trees, as one would expect in such a situation, are stunted and their growth form is the same in both woods; instead of the usual single trunk, each tree has a number of more or less upright "trunks" springing from a common stool. This type of growth form has been described for some very similar *Quercus robur* woods situated on Dartmoor (2) and will be discussed more fully later.

In order to bring out the main points of interest presented by the two woods we will now pass on to consider them separately and in greater detail.

#### THE BIRKRIGG OAKS.

This wood is the smaller of the two, being about 400 yds. long and 150 yds. across its widest part. Taking into account the slope of the ground, the area, according to the 6-inch Ordnance Survey map, is about 8 acres. A near view of this wood is shown in Pl. XIII, Phot. 3, and it can be seen that at its western end (to the left of the photograph) it is cut into a number of narrow strips by stretches of scree, while to the east the main wood ends abruptly except for three or four outlying trees standing some yards away along the slope. About two hundred yards to the east of the main association is a further small patch of oaks, the trees of which however are more widely spaced than those in the main wood; this patch is faintly discernible on the extreme right of Pl. XIII, Phot. 3. The wood is bounded along its upper margin by a narrow belt of open oak scrub at an altitude of about 1400 ft. Below, the trees disappear more or less abruptly at about 1150 ft. The average slope of the ground on which the wood stands is approximately 30° from the horizontal.

On entering the wood one is at once struck by the characteristic growth form of the trees; this is shown in Pl. XIII, Phot. 1. They (each with several "trunks" springing from a common stool) give one the impression that coppicing must have taken place at some time. These "trunks" for the most

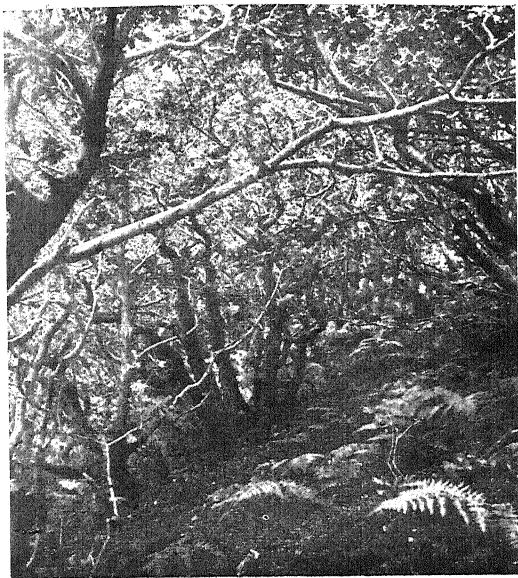


Photo 1. General view of interior of the Birkrigg wood showing the growth form of the trees, and the nature of the ground flora. Here *Vaccinium myrtillus* is abundant, and *Pteridium* frequent.



Photo 2. Base of a small tree in the Birkrigg wood, the upper portion of which has died. Note young suckers springing up.



Photo 3. General view of the Birkrigg oaks. Note the screes cutting up the western end of the wood.

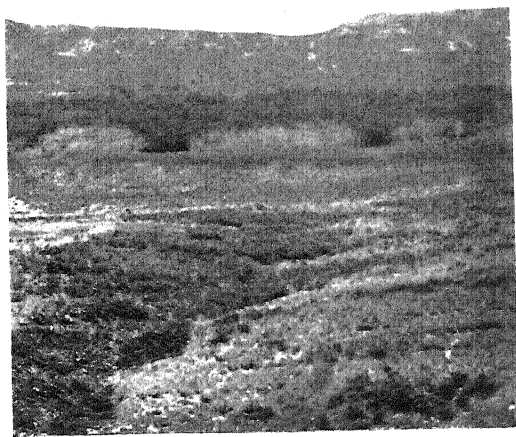


Photo 4. View of the Birkrigg wood from the bottom of the valley showing the areas burnt in 1922. (These burnt areas appear lighter in tone than the rest of the wood.)



part vary in girth between about 6 ins. and 18 ins., and the trees, which are spaced approximately 6 ft. to 12 ft. apart grow, on an average, to a height of some 12 ft. The result is that for the most part a close canopy is formed, casting a considerable shade.

As has already been stated, all the oaks so far examined in the wood have proved to be *Quercus sessiliflora*, and mixed with them are occasional trees of mountain ash (*Sorbus aucuparia*); a few seedlings of both oak and mountain ash have also been observed. No acorns have so far been seen, although there is no reason to believe that they are not produced.

The ground flora in the main central portion of the wood forms a decidedly open association and in many parts there is a tendency for the surface soil to become transformed into scree by the washing away of the finer particles. In such situations, the foot-hold maintained by the plants is of a precarious nature, and signs of the struggle, in which they are involved, with the physiographic factors of the habitat, are easily recognisable.

A general survey of the ground flora of the main wood shows it to have in its composition a large percentage of heath forms. The general and local composition of the ground flora is obviously closely related to the shade cast by the oaks and the increased humidity of the atmosphere brought about by their presence. For instance, bryophytes are abundant, and in the more strongly shaded parts they frequently assume local dominance, the most abundant species being *Dicranum scoparium*, *Hypnum cupressiforme*, and *H. schreberi*. *H. cupressiforme*, var. *filiforme* completely covers the lower parts of most of the tree trunks, while on the upper branches epiphytic cushions of *Ulota crispa* are abundant everywhere, as also are various lichens. As regards the higher plants in the ground flora we find all stages between an absence of any distinctly dominant species, and complete dominance of *Pteridium aquilinum*, *Vaccinium myrtillus*, or *Calluna vulgaris*. Of these, *Pteridium* is most frequently dominant in the open spaces where lighting is good, although occasionally its place as dominant is partially or wholly taken by *Calluna*. *Vaccinium myrtillus*, which is, like *Pteridium*, frequent throughout the wood, commonly becomes dominant in the shade of the oaks.

The general composition of the ground flora of the wood is as follows:

<i>Pteridium aquilinum</i>	f. (d. in clearings)	<i>Teucrium scorodonia</i>	o.
<i>Calluna vulgaris</i>	o. (f. to d. in clearings)	<i>Hypericum pulchrum</i>	r.
<i>Vaccinium myrtillus</i>	f. to d.	<i>Quercus sessiliflora</i> (seedlings)	v.o.
<i>Oxalis acetosella</i>	o. to f.	<i>Sorbus aucuparia</i> (seedlings)	o.
<i>Galium saxatile</i>	o. to f.	<i>Deschampsia flexuosa</i>	f.
<i>Campanula rotundifolia</i>	o.	<i>Agrostis canina</i>	o. to f.
<i>Viola riviniana</i>	o.	<i>Anthoxanthum odoratum</i>	f.
<i>Potentilla erecta</i>	o.	<i>Festuca ovina</i>	o.
<i>Veronica serpyllifolia</i>	o.	<i>Blechnum spicant</i>	o.
var. <i>humifusa</i>	o.	<i>Dryopteris filix-mas</i>	o.

## Bryophyta:

<i>Andreaea petrophila</i>	<i>Plagiothecium silvaticum</i>
<i>Antitrichia curtipendula</i>	<i>Plagiothecium denticulatum</i>
<i>Brachythecium purum</i>	<i>Polytrichum formosum</i>
<i>Bryum capillare</i>	<i>P. gracile</i>
<i>Camptothecium sericeum</i>	<i>P. juniperinum</i>
<i>Campylopus schwarzii</i>	<i>Rhacomitrium heterostichum</i>
<i>Dicranum fuscescens</i>	<i>R. lanuginosum</i>
<i>D. majus</i>	<i>Thuidium tamariscinum</i>
<i>D. scoparium</i>	<i>Ulota crispa</i>
<i>Eurhynchium praelongum</i>	<i>Alicularia scalaris</i>
<i>Hylocomium loreum</i>	<i>Diplophyllum albicans</i>
<i>H. splendens</i>	<i>Lophocolea bidentata</i>
<i>Hypnum cupressiforme</i>	<i>Lophozia alpestris</i>
	<i>L. barbata</i>
<i>H. schreberi</i>	<i>L. hatcheri</i>
<i>Mnium hornum</i>	<i>Marsupella emarginata</i>

Above and below the wood are associations of heath plants, dominated by *Calluna* or *Pteridium*. Above, *Calluna* is dominant except over small areas, where *Vaccinium myrtillus*, which is everywhere an abundant associate, locally assumes dominance. *Pteridium* is frequent, especially where the soil tends to become unstable and to pass into scree. An interesting feature of this upper association is the presence of frequent young mountain ash trees. These young trees are seldom more than 18 ins. or 2 ft. in height, owing, without doubt, to the periodic burning of the *Calluna*.

Immediately below the wood, for about the first six yards after leaving the trees, *Pteridium* dominates. Lower down, *Calluna* is dominant and lower still, down to the stream, *Pteridium* again is dominant.

Along the hillside in an easterly direction from the wood *Pteridium* is, except in the spring flushes, dominant on the lower slopes up to about 1100 ft. Above this altitude the *Pteridium* thins out, and dominance is assumed by *Calluna*, or shared by *Calluna* and *Erica cinerea*. Higher still, between 1250 and 1500 ft. the soil in many places, owing to the steep slope and rapid denudation, becomes unstable and supports open or closed associations either of practically pure *Vaccinium myrtillus* or *V. myrtillus* mixed with *V. vitis-idaea* with here and there an occasional *Pteridium* frond.

*The Causes of the "Coppiced" Appearance of the Trees.*

There is evidence that the apparently "coppiced" growth form of the trees may have arisen in three ways:

(1) *By artificial coppicing.*

No evidence was obtained to show that the Birkrigg Oaks have been artificially coppiced within recent times, as in the case of the Keskadale Oaks (see p. 299).

(2) *By burning.*

In July, 1923, while examining the lower margin of the wood, it was observed that the *Calluna* and *Pteridium* had been burnt sometime during the autumn of 1922. The burning had extended for some distance into the

wood and had killed the upper parts of the trees. The general appearance of the damage caused by this fire is shown in Pl. XIII, Phot. 4, which is a view of the wood taken from the bank of the stream, Rigg Beck, immediately below. In this photograph the burnt areas show as lighter patches along the lower margin of the wood. It was found, on examining these burnt trees, that only their upper portions had been killed, and that their underground stools had escaped injury and had produced a growth of vigorous young shoots (see Pl. XIV, Phot. 5). This has been found frequently to occur after firing of the heather, in the case of trees growing on Hindhead Common in Surrey (5).

In July, 1924, the wood was again examined, and further burnt areas were noted. One of the narrow belts of trees, cut off by scree from the western end of the main wood, was found to have been on fire sometime during the previous autumn. Again a similar state of affairs to that described above was found. Most of the oaks had been completely killed in their upper parts, while from the stools numerous young suckers had sprung up.

In this portion of the wood, the oaks are more widely spaced than in the main wood, and the resulting absence of dense shade allows the *Calluna* and *Pteridium* to grow luxuriantly. This thick growth of *Calluna* provides abundance of readily combustible undergrowth which, with the accompanying danger of fire, is to a large extent absent from the denser main wood.

The seral changes in the subere initiated by this burning of the undergrowth were found to be well shown in the already-mentioned small patch of oaks which lie to the east of the main wood. Here the trees are widely spaced, allowing *Calluna* to become dominant in the ground flora. The western portion of this patch showed unmistakable signs of having been burnt within the last twelve months. Here again the oaks, in their upper parts, were in almost every case quite dead, but had produced the usual dense growth of suckers. Pl. XIV, Phot. 6, shows this part of the wood at the time of writing the present account. In the foreground can be seen the dead *Calluna* stems. An examination of the new ground flora in this region showed that the plants present could be divided into two categories: (a) those which had not had their underground parts killed by the fire, and which were springing up again from these old stocks, and (b) those species which had been more or less completely killed, and which were reappearing as seedlings. Below are lists of these two groups with their frequencies as they occurred on this burnt area.

(a) Springing from old stocks:

<i>Vaccinium myrtillus</i>	a.	<i>Deschampsia flexuosa</i>	o.
<i>V. vitis-idaea</i>	f.	<i>Sorbus aucuparia</i>	o.
<i>Pteridium aquilinum</i>	o. to f.	<i>Blechnum spicant</i>	o.
<i>Erica cinerea</i>	o.		

(b) Seedlings:

<i>Calluna vulgaris</i>	f.	<i>Anthoxanthum odoratum</i>	o. to f.
<i>Erica cinerea</i>	o. to f.	<i>Deschampsia flexuosa</i>	o.
<i>Galium saxatile</i>	f.	<i>Potentilla erecta</i>	o.

From these lists it will be seen that one of the most conspicuous effects of the burning, upon the ground flora, is the same as has been observed by Elgee (3)<sup>1</sup> on the Yorkshire moors, after the burning of *Calluna*; viz. *Vaccinium myrtillus* becomes the most abundant constituent. A later stage in the subseres was found at the eastern end of this patch where the main shoots of the trees were from  $\frac{1}{2}$  to  $\frac{3}{4}$  in. in diameter. As far as could be ascertained, the annual rings present in the older shoots of these trees, indicated some five or six years' growth. Thus the burning, in this part, must have taken place five or six years previously. The associated ground flora, dominated by *Vaccinium myrtillus*, and containing frequent well-grown plants of *Erica cinerea* (see Pl. XIV, Phot. 7), is given in the following list:

<i>Vaccinium myrtillus</i>	d.	<i>Deschampsia flexuosa</i>	f.
<i>V. vitis-idaea</i>	f. to a.	<i>Anthoxanthum odoratum</i>	f.
<i>Calluna vulgaris</i> (mostly young plants)	f.	<i>Galium saxatile</i>	o. to f.
<i>Erica cinerea</i>	f.	<i>Potentilla erecta</i>	o.
		<i>Lycopodium alpinum</i>	o.

The *Calluna* here, though not yet approaching the position of dominance, is rapidly making headway.

On the above area were a number of small patches which obviously escaped burning during the last fire. In these, the trees had the same general appearance as those in the main wood, although their existing shoots were considerably younger. The ground flora of these patches was dominated by *Calluna*, associated with frequent plants of *Erica cinerea*, and can be clearly seen in Pl. XIV, Phot. 8. Its composition was found to be as follows:

<i>Calluna vulgaris</i>	d.	<i>Galium saxatile</i>	o.
<i>Erica cinerea</i>	f.	<i>Potentilla erecta</i>	o.
<i>Vaccinium myrtillus</i>	f.	<i>Deschampsia flexuosa</i>	o.
<i>V. vitis-idaea</i>	f.	<i>Pteridium aquilinum</i>	o.

In consideration of the above observations it is evident in the more open parts of the wood that the apparently "coppiced" growth form of the trees can be occasioned by firing of the heather. Such a cause would be more rarely operative in the denser areas where the undergrowth is sparse and poorly developed.

### (3) *By natural death of the upper shoots.*

A possible natural cause of the apparently "coppiced" growth form of the trees is suggested by their appearance.

Many of the main shoots of the oaks are in an extremely unhealthy state, while others are quite dead. Here, although not to the same extent as was observed in the burnt areas, there is a marked tendency for young shoots to be produced from the bases of the trees. These small shoots are of various ages and are more abundant on the trees with dying or dead upper parts (see Pl. XIII, Phot. 2). It is difficult to arrive at any certain conclusion concerning the death of the upper parts of the trees in these denser regions of the wood.

<sup>1</sup> Other references to the effects of burning of *Calluna* are Nos. 4, 5, 7, 8, given in the list at the end of this paper.





Photo 5. One of the trees in the central burnt area shown in Pl. XIII, Photo 4. Note the suckers springing from the stool, which has retained its vitality, while the old upper shoots have been killed by the fire.



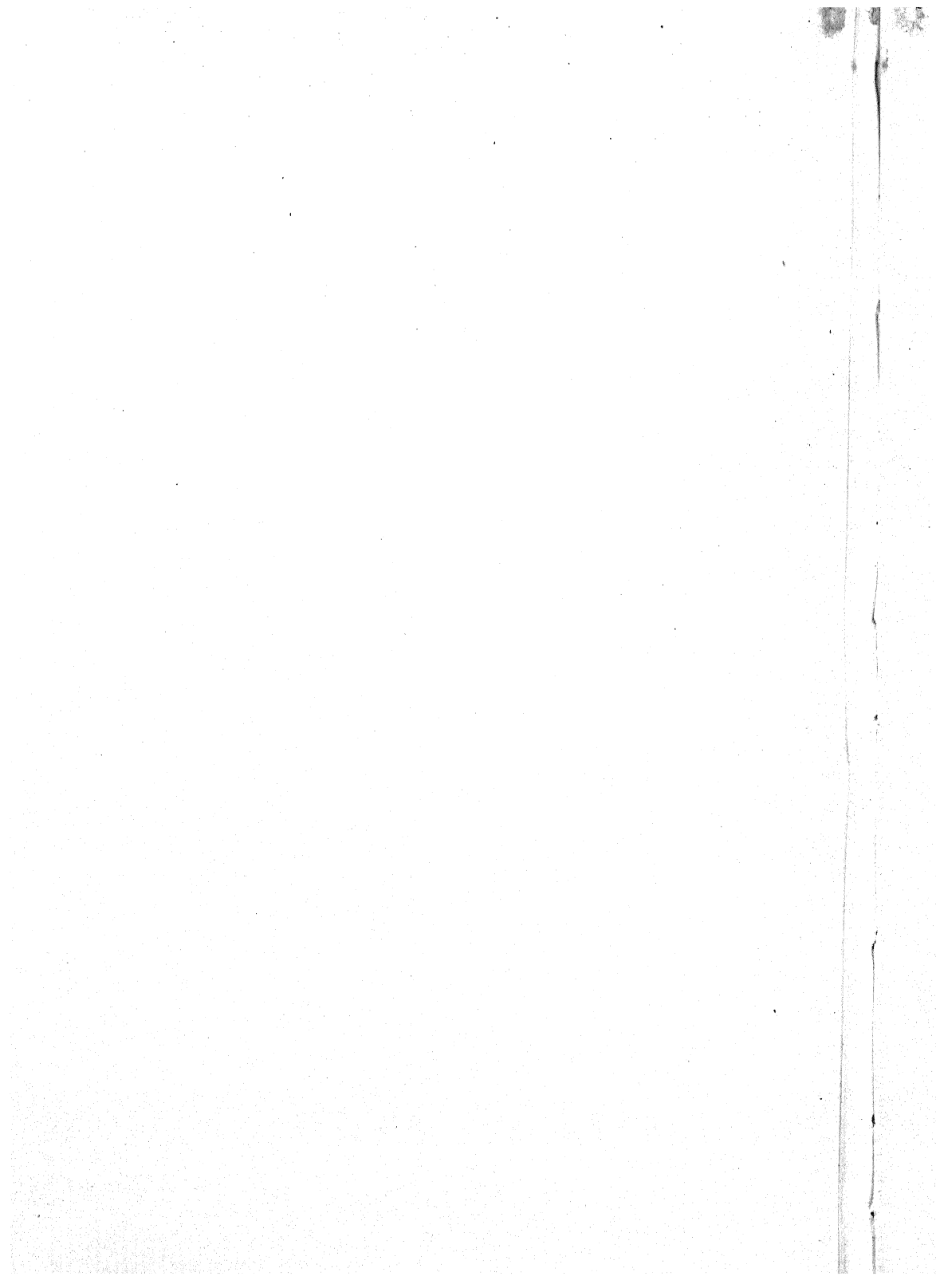
Photo 6. View taken in the patch of oaks to the east of the main Birkrigg wood showing the appearance of trees and ground vegetation during the first season after burning.



Photo 7. A portion of the eastern patch of the Birkrigg Oaks (see p. 290) where burning took place five or six years previously. Note dominance of *Vaccinium*, and the large plants of *Erica cinerea* in the ground flora.



Photo 8. Another portion of the eastern patch of Birkrigg Oaks where burning has not taken place. Note the dominance of *Calluna*.



All the oaks are very markedly attacked by fungi, the most conspicuous of which is *Dichaena quercina*. This fungus is present in the imperfect state which very commonly infects young oaks in all parts of the country. It is generally reputed to cause little or no damage to the trees, but in this wood, where they are undoubtedly growing under very limiting habitat conditions, this usually harmless organism, may become an important lethal factor. Nevertheless, whatever the specific causes of the death of the older branches may be, the fact remains that they are, in many places, dying, while the stools which retain their vitality produce a fresh growth of young shoots. In this way it seems that the apparently "coppiced" growth form may, in such situations, arise quite naturally.

#### THE KESKADALE OAKS.   ▼

This wood occupies a site very similar to that of the Birkrigg Oaks. Its position however is more accessible than that of the latter as Keskadale is a valley of considerable size with a number of farms in it; also the main Newlands road from Keswick to Buttermere runs through it. For this reason one is rather surprised to find that the wood covers some 19 acres of ground, i.e. it occupies an area more than twice as great as that of the Birkrigg Oaks. It stretches about 600 yds. along the south-east slope of Ard Crag, and is approximately 300 yds. across at its widest part. The upper limit of the wood proper lies at an altitude of about 1500 ft., although stunted oaks grow at still higher levels on the crags above. The lower margin lies a little below the 1000 ft. contour.

The slope on which this wood stands is somewhat steeper than that occupied by the Birkrigg Oaks, making on an average an angle of about  $40^{\circ}$  with the horizon. The soil is of the same type as in the other wood, and in places rapid denudation is taking place. This is particularly noticeable at the north-east and south-west ends of the wood, which is however, nowhere cut into isolated strips by scree. To the south-west of the centre of the upper margin, the slope becomes much steeper and passes into precipitous crags. The oaks continue to grow for some distance up the crags, although here, as one would expect, they are very stunted.

In the centre and lower parts of the wood the trees correspond in appearance with those of the Birkrigg wood but are a little taller on an average. Along the upper margin however, just below the crags, they grow to a height of some 30 ft., with a girth of about 36 ins. These variations in the tallness of the trees in different parts of the wood are of considerable interest as they are definitely related to variations in the slope of the hillside. If the wood is viewed from some distance along the valley, the tops of the trees form a very even surface which does not appreciably deviate from its general regularity, with minor, although abrupt, changes in the contour of the slope. A similar regularity of surface is mentioned by Worth (2) in connection with Piles Wood on Dartmoor.

It is also noticeable when the Birkrigg Oaks are viewed from a distance, although here the regularity of the slope of the hillside and the corresponding uniformity in the heights of the trees render its significance less evident.

There can be little doubt that the primary cause of the trees growing up to this "general vegetation level" (11) lies in the effect of wind. Fig. 2 is a

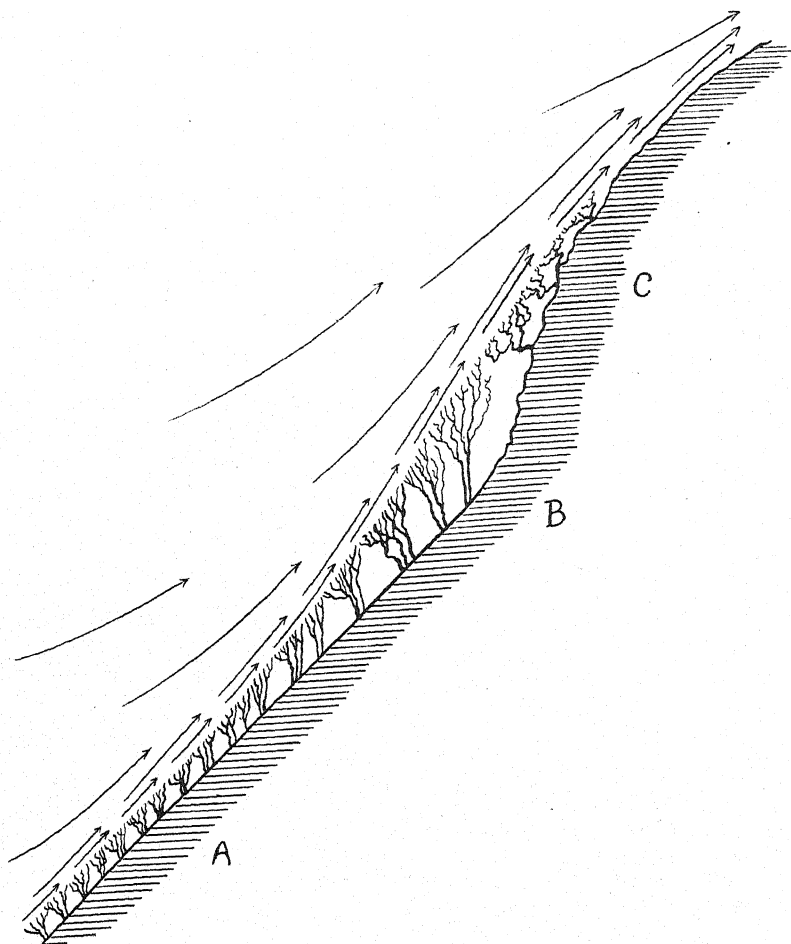


FIG. 2. For description see text.

diagrammatic bisect through the upper part of the Keskadale wood. On this diagram, the central region of the wood, where the slope is fairly uniform, is indicated at *A*. At *B*, just below the crags, there is, relatively speaking, a hollow in the hillside, and here the trees grow taller than those at *A*, thus preventing any correspondingly sudden variation in the "general vegetation level." At *C*, on the crags, for a similar reason, the trees are very much stunted. The arrows on the diagram indicate the approximate mean path taken by

those winds which have the most serious limiting effect upon the vegetation of this slope.

The effect of wind, as a limiting factor, upon vegetation has long been recognised, and is discussed at some length by Yapp (11) in connection with marsh vegetation.

The Keskadale wood, as regards its floristic composition, bears a close general resemblance to the Birkrigg wood. The trees are apparently all *Quercus sessiliflora*, except for an occasional *Sorbus aucuparia*. A few mountain ash, but no oak, seedlings were observed, although the latter was possibly due to insufficient searching. The composition of the ground flora was found to be as follows:

<i>Pteridium aquilinum</i>	f. to a.	<i>Teucrium scorodonia</i>	o.
<i>Calluna vulgaris</i>	o. to l.a.	<i>Hypericum pulchrum</i>	o.
<i>Vaccinium myrtillus</i>	l.f.	<i>Rubus</i> sp.	o.
<i>Oxalis acetosella</i>	o. to f.	<i>Sorbus aucuparia</i> (seedlings)	o.
<i>Galium saxatile</i>	o. to f.	<i>Deschampsia flexuosa</i>	f. to a.
<i>Campanula rotundifolia</i>	o.	<i>Agrostis canina</i>	f. to a.
<i>Viola riviniana</i>	o.	<i>Anthoxanthum odoratum</i>	f. to a.
<i>Potentilla erecta</i>	o. to f.	<i>Festuca ovina</i>	o.
<i>Veronica serpyllifolia</i> var. <i>humifusa</i>	o.	<i>Blechnum spicant</i>	o.

### Bryophyta:

<i>Antitrichia curtipendula</i>	<i>Hypnum cupressiforme</i>	<i>Racomitrium heterostichum</i>
<i>Brachythecium rutabulum</i>	" var. <i>filiforme</i>	<i>R. lanuginosum</i>
<i>Bryum capillare</i>	" var. <i>ericetorum</i>	<i>R. sudeticum</i>
<i>Campylopus fragilis</i>	<i>H. schreberi</i>	<i>Ulota crispa</i>
<i>Dicranum majus</i>	<i>Plagiothecium denticulatum</i>	<i>Diplophyllum albicans</i>
<i>D. scoparium</i>	<i>P. silvaticum</i>	<i>Lophozia barbata</i>
<i>Eurhynchium praelongum</i>	<i>Polytrichum aloides</i>	<i>L. floerkii</i>
<i>Hylocomium loreum</i>	<i>P. formosum</i>	<i>Scapania curta</i>
<i>H. splendens</i>	<i>P. piliferum</i>	

If this list is compared with that for the other wood given on p. 291 it will be seen that the two correspond closely. One point of some interest, which is not brought out by the above list, is in connection with the distribution of *Calluna* and *Vaccinium myrtillus*. As one passes upwards through this wood in a westerly direction from the lower side of the north-eastern end, *Vaccinium myrtillus* is found to be entirely absent over the lower and central regions, and *Calluna* only occurs very sparsely in the more open spaces between the trees. In the upper and more westerly parts, as one approaches the crags, *Vaccinium* appears, and grows abundantly in the shade of the trees, and *Calluna* becomes dominant in the open, unshaded areas, and grows profusely associated with *Erica cinerea* on the crags.

Below the lower margins of the wood, a few more or less isolated trees occur and most of these have a curious, very thick, bushy growth of small shoots round their bases (see Fig. 3). These shoots probably owe their origin, in the first place, either to cutting, or to burning. It is obvious, however, that their thick, bushy growth is the result of sheep grazing, as considerable numbers of these animals feed on the hillside.

Immediately below the wood is a narrow zone of grass heath with no markedly dominant species, and below this, *Pteridium* becomes dominant. At the north-east end of the wood the *Pteridietum* extends right up to the trees,



FIG. 3. An oak tree just below the Keskadale wood showing bushy growth caused by sheep grazing.

and, as on Causey Pike, running along the slope from the wood, in a north-easterly direction, is a zone of *Pteridietum* stretching from the road below up to about the level of the trees. Above this *Calluna* tends to become dominant.

#### CONCLUSION.

From the foregoing brief descriptions it will be seen that these two woods present a number of features of ecological interest. From a consideration of habitat conditions, as regards altitude, slope of ground, soil, etc., there seem good reasons for believing that we have here authentic relicts of a primitive forest which at one time was of much greater extent. This idea of more extensive woodland is supported by some of the place-names of the district in the immediate neighbourhood of the existing woods. For instance, we have Birk Rigg, Birkrigg Brow, and Birkthwaite. These may either refer to primitive upland birch woods, or to birch woods appearing after the felling or degeneration of oak woods. Again, along the ridge, about half a mile to the east of the Keskadale Oaks is Aikin Knot, while below, in the valley is Aikin House. The Aikin here is obviously derived from Oaken. The distribution of *Pteridium* along the hillsides, beyond the limits of the present woods, is also significant in connection with the supposition that this plant often occupies the site of former woodland (8). Further, there is little room for doubt that the larger

valleys formerly supported oak woods, although these lower lying valley woods, judging from the trees at present growing in the hedgerows, were probably largely dominated by *Quercus robur*.

That a very considerable amount of human interference has taken place within historic times is more than likely, and, although no information concerning the cutting of the Birkrigg Oaks in recent times was obtained, it was definitely ascertained, indirectly, from one of the older inhabitants of the district, that the Keskadale Oaks were cut, about a hundred and fifty years ago, for the purpose of obtaining bark for tanning. Most of the trees, therefore, in this latter wood, are the result of regeneration by the development of suckers from the old stools. This fact would here explain the "coppiced" growth form of the trees. The fact that this growth form can arise in other ways, and may be an entirely natural result of certain habitat conditions is of some interest. This is especially so in the light of parallel cases described in connection with very similar woods situated on Dartmoor (2). The exceptional altitude of these woods is of considerable interest in view of their proximity to the sea. Brockmann (1) has shown that, in the Northern Hemisphere, the presence of large land masses has the effect of pushing the tree limit nearer to the pole, while the presence of oceans has the opposite effect. He has also shown that, in alpine regions, the tree limit occurs at a higher altitude where climatic conditions are of a continental nature, than is the case where oceanic climatic conditions prevail. Taking into account Brockmann's conclusions, one would expect to find that these woods, and also those on Dartmoor, occupied positions of a somewhat lower altitude than upland woods of the more inland parts of Great Britain. From this it would seem probable that the upward limits of *Quercetum sessiliflorae* and *Quercetum roburis* in this country occur at higher altitudes than has usually been assumed (about 1000 ft. for *Quercetum sessiliflorae* (8)). The southern aspect of the slopes on which these woods occur will also have a marked influence upon the altitude to which the trees ascend (9). A limiting factor however is introduced by the position of the woods, which are exposed to the action of cold east winds, but these, judging from conditions existing in the case of the Dartmoor woods (2) have a less serious effect upon tree growth than the south-westerly Atlantic gales.

In conclusion, it seems possible that these two undoubtedly ancient woods may, under existing conditions, eventually disappear, owing to the almost entire failure of natural regeneration by means of seedlings (10). There is very little evidence to show, at present, that they are not stable associations, but, though regeneration by means of suckers may quite successfully continue for many years, one cannot conceive of its being effective over an indefinite period.

I am indebted to the Joint Standing Committee for Research of The University of Birmingham for providing a grant to defray the expense of one of the plates illustrating this paper.

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# PLANT STRUCTURE AND ENVIRONMENT WITH SPECIAL REFERENCE TO FOSSIL PLANTS

BEING THE PRESIDENTIAL ADDRESS TO THE  
BRITISH ECOLOGICAL SOCIETY  
DELIVERED JAN. 10TH, 1925

By F. E. WEISS.

In my presidential address to the botanical section of the British Association, meeting at Portsmouth in 1911, I drew attention to the statement of Dr D. H. Scott at the conclusion of his *Studies in Fossil Botany* that "the subject of the biology of fossil plants as illustrated especially by their physiological anatomy, offers a wide and promising field of research." I ventured at the time to make some remarks on the general biological conditions, under which the plants of our Coal Measures lived, based upon some of the more striking features of their anatomical structure. If I refer to this matter again it is with a view to stimulate interest in this fascinating problem and to help to extend its study. That this aspect has not been neglected by palaeobotanical observers is evident from the vivid account given by Kidston and Lang<sup>1</sup>, not only of the conditions under which their remarkable Devonian Psilophytales grew, but also of the nature of the cataclysm which ended in their perfect preservation *in situ*. These speculations are based in part on their normal anatomical structure, in part on certain apparently pathological features which their tissues exhibit. Quite recently too Gothan<sup>2</sup> has dealt with the biological features of plants of the successive geological formations.

I shall confine myself to-day to plants of our British Coal Measures with which I am more familiar and from which, owing to their less perfect preservation, a good deal more requires to be learnt. In this direction Hamshaw Thomas<sup>3</sup> has shown us a useful line of advance by his investigations of the leaves of Calamites. After a careful comparative account of the various forms of Calamitean leaves, he considers also the probable habitat and climate under which these carboniferous plants grew. I will begin my consideration of the subject to-day with the structure of the roots, not because I do not equally value the testimony that can be gathered from the leaves, but because the evidence of both sets of organs requires to be taken into consideration in determining the physiological needs and the biological conditions of the plant.

<sup>1</sup> Kidston, R. and Lang, W. H. "On Old Red Sandstone Plants showing Structure," Part V. *Trans. Roy. Soc. Edinburgh*, 52, 1921.

<sup>2</sup> Gothan, W. *Palaeobiologische Betrachtungen über die fossile Pflanzenwelt*, 1924.

<sup>3</sup> Thomas, H. "On the leaves of Calamites." *Phil. Trans.* 202, 1911.

The young roots of Calamites are in structure typical of those of a marsh or aquatic plant. So close indeed is their resemblance to the latter that the name of Myriophylloides was given to them by Cash and Hick<sup>1</sup> before it was known that they were the roots of Calamites. Apart from the vascular tissues which have a typical root structure, they are characterised by very large air spaces between the radial rows of cells of the mid-cortex. An interesting feature of this lacunar cortex, to which little attention seems to have been paid, is the fact that in many of the roots a curious bulging of some of the cells seems to have occurred (see Scott's *Studies*, Fig. 17), which at first suggests that protuberances are formed for the purpose of keeping open the intercellular passages of the very delicate roots, since the latter have no obvious septa. In a few roots I have, however, observed that the spaces may become almost entirely obliterated by such cells, though no doubt small intercellular passages may have been retained. This might therefore represent a method of general strengthening of the lacunar tissue. Another suggestion that might be advanced is that roots of this nature were growing in a drier medium than was normally the case, or were required to be of firmer texture, perhaps to act as stilt-roots. On the whole, however, it seems to be a common development in these roots, and represents an occurrence which I do not know to be paralleled among recent plants.

What happened to the lacunar tissue in old roots in which the vascular tissue had undergone secondary thickening is not clearly known. But that the older roots were provided with aerenchyme is obvious from Renault's figure reproduced in Scott's *Studies* (Fig. 16, p. 38). It is possible that the radial rows of cells there shown may have arisen by a stretching of the primary lacunar tissue, but there is also a possibility that their origin may have been a secondary one. The appearance of this tissue in a root with secondary thickening resembles very closely the structure shown by a pneumathode of *Bruguiera*, though I do not wish to suggest that these roots had primarily a similar function. Attention has been drawn by various observers to the root-hairs generally with dilatated base which occur on the rhizomes of various Equiseta. No such root-hairs have been found on Calamite roots and it is of course possible that they may not have possessed any root-hairs, as is the case with many aquatic plants. The external layer of the roots with thick outer walls, which was termed the epidermoidal layer by Williamson, may be, as Scott indicates, comparable with the exodermis of many recent roots, but may possibly be the true epidermis, which may subsequently have become thickened. We must, however, bear in mind that, as Mrs Arber states (*Water plants*, p. 208), "in the roots of water plants the piliferous layer and the layer immediately below it are often cuticularised." Sauvageau<sup>2</sup> also states

<sup>1</sup> Cash, W. and Hick, T. *Proceedings of the Yorks. Geol. Polytech. Soc.* 1881.

<sup>2</sup> Sauvageau, C. "Sur les feuilles de quelques Monocotyledones aquatiques." *Annales des Sci. Nat. Sér. VII, Bot.* 13, 1891.

that in the case of the leaves of submerged *Potamogetons* the cuticle offers no obstacle to the entry of liquids as proved by plasmolysis experiments in which the whole leaf was used. As regards the stems of the *Calamites* our knowledge of its aerating tissue is more limited, largely owing to the fact that the layers lying outside the vascular tissue are generally not well preserved.

All stems, however, show a hollow pith formed probably by disorganisation of its tissues, but bridged over at the nodes by a definite septum. Whether this septum, which is comparatively substantial, had any fine passages for air or not we do not know. No indications of such passages are apparent, but the matter is worth further investigation. The young stem in which we might look for a lacunar cortex has so far not revealed any such structure. The specimen figured by Hick and by Seward (*Fossil Plants*, 1, p. 315) shows an internal cortex of large parenchymatous cells and an outer one of smaller cells, some of which are thickened, but the irregular outline of the stem may indicate that we have not got the natural boundary of the stem.

There is certainly nothing in *Calamites* as striking as the vallecular canals in the cortex of the various species of *Equisetum*. On the other hand, in the older stem figured by Seward (*Fossil Plants*, Fig. 74 B), in which the epidermal layer is preserved, there are in the outer cortex bands of sclerenchymatous cells alternating with spaces which might have been occupied by more delicate parenchyma as suggested by Seward, but which might possibly have been intercellular passages similar to the vallecular canals of *Equisetum*. A further investigation of the best preserved material might throw light on this subject.

It is perhaps of interest to note that in *Palaeostachya* nine such "canals" alternating with the carinal canals have been described by Hickling<sup>1</sup> in the sclerotic disc of the nodes (see also Scott's *Studies*, Fig. 27).

In the vascular cylinder we have of course, in almost all *Calamitean* stems the very characteristic carinal canals associated with the protoxylem elements and indeed formed by their disorganisation according to Scott's description (*Studies*, Fig. 6). To what extent, if any, they are concerned with the aeration of the tissues is quite uncertain.

We have still to consider the large central hollow canal formed by the disintegration of the pith. Such hollow pith is of course by no means limited to aquatic plants and may have more to do with the efficient mechanical distribution of the tissues on the principle of a hollow cylinder, and not possess any physiological significance. The transverse septa which cut off the central canal of each internode from the next, thus forming apparently air-tight compartments, would seem to militate against the latter functioning in any such capacity as that of aeration. I shall, however, refer to this matter later on.

So far no stomata—such conspicuous objects in the *Equiseta*—have been found in the epidermis of the internodes of the stem of the *Calamites*.

<sup>1</sup> Hickling, G. "The Anatomy of *Palaeostachya vera*," *Ann. of Bot.* 21, 1907.

but it is possible they may yet be found, though it may be that the provision for the intake of air through the leaves in Calamites compensates for the absence or infrequency of stomata on the stem. Nor have any lenticels been observed in the older stems such as one might expect on stems with secondary thickening, particularly if there was great need for conduction of air.

Taken in conjunction with the facts elucidated by Thomas for the structure of the leaves, which contain wide intercellular spaces between the palisade cells, the anatomical characters of the root indicate the development of an extensive system of aeration, such as is characteristic of aquatic plants. Of the recent *Equiseta*, the nearest living relations of the Calamites, a number grow under aquatic conditions, though other species affect drier situations. In some of these, *E. arvense* for example, the aerating tissues show a decreased development, particularly the intercellular spaces in the root which are so largely developed, as in the Calamite root. Still we must regard the *Equiseta* as very adequately supplied with air-conducting passages since Unger<sup>1</sup> has shown that, if a stem of *Equisetum limosum* or *E. hyemale* is plunged into water and air is blown into the cut base, bubbles will be given off through the stomata in the stem. With a little more force an even better effect can be obtained with the sterile shoots of *E. maximum*. Unfortunately, we cannot make similar experiments with fossil plants. It remains for us to trace, as far as that is possible, the continuity of intercellular passages from the leaves into the stem and hence down into the roots. For this a detailed search is required. But with time and patience this may yet be done. We do not know for instance what happens at the nodes of the Calamite stem. The large central canal of each internode would seem to be completely cut off from that above and below by the nodal septum. But it is possible that the central cavity may be connected even in comparatively old plants, in which it is surrounded by a massive central cylinder with intercellular spaces in the cortex. I am inclined to think that Williamson's "infranodal canals," which pass in the primary medullary rays through the whole extent of the secondary wood, may have been part of the aerating tissues of the older stems. In well-preserved specimens, however, no actual canals are seen, but a small-celled tissue which has been regarded by some investigators as of a secretory nature. But the frequent defectiveness of the cells suggests to me a similarity to an aerating tissue such as is found in lenticels, though here we have communication with the exterior rather than with the centre of the stem. In this connection it is of interest to note that Jeffrey<sup>2</sup> has found structures similar to infranodal organs of Calamites in such marsh plants as *Potentilla palustris* and *Polygonum amphibium*. That the leaves have certain xerophytic characteristics, as Thomas has shown, does not invalidate the conclusion that the

<sup>1</sup> Unger, "Beitraege zur Physiologie der Pflanzen." *Sitzungsber. d. Kais. Akad. d. Wiss.* 25, 1857.

<sup>2</sup> Jeffrey, E. C. "On Infranodal Organs in Calamites and Dicotyledons." *Annals of Bot.* 15, 135.

Calamites were rooted in a watery medium. Even Henslow<sup>1</sup>, in his article "On the Xerophytic Characters of Coal Plants," admits that the Equisetales were decidedly hygrophytic. But the rest of the palaeozoic plants, like their modern representatives, he asserts, were xerophytic. This, he says, "implies that the majority of the coal-plants did not grow in swamps."

Let us now examine some of these other plants in their turn. Taking the Lycopodiales first, we will start here too with the absorptive organs. These are borne in the case of *Lepidodendron* and *Sigillaria* on the Stigmarian axes, the morphological nature of which has been so much discussed. The rootlets these axes bear would certainly be regarded by an unbiassed observer as suited to an aquatic habitat. They are devoid of root-hairs, and their most characteristic feature is the lacunar nature of the middle cortex, the delicate tissue usually defective in petrified material and replaced by a wide intercellular space, so that the monarch vascular cylinder is either completely free from the outer cortex, or slung up to it by a comparatively narrow band of parenchymatous cells. The only root of recent plants which offers a close comparison with the Stigmarian appendages is that of *Isoetes*, a truly aquatic plant and one which is in all probability its nearest living relative. It is of interest to note that in one type of Stigmarian rootlet<sup>2</sup> the middle cortex was of a closer and firmer texture and resembles a mass of interlacing cells. Probably this tissue was provided with small intercellular spaces and possibly it may have arisen by a secondary change in the lacunar tissue in the same way as I mentioned a filling up of the lacunae takes place in some roots of Calamites. But though this particular rootlet in question does not indicate an aquatic habit, we may safely say for the Stigmarian rootlets as a whole that they were adapted to a watery medium.

The very defective middle cortex, together with the monarch nature of the vascular cylinder, seems to have necessitated the development of a special structural device for transmitting the water absorbed by the epidermis to the vascular cylinder which, as far as I know, is unique in the vegetable kingdom. This is the development of delicate radially running strands of tracheids<sup>3</sup> linking up the protoxylem group of the central cylinder with a system of tracheids found in the outer cortex.

The Stigmarian axis from which the rootlets spring, shows like the latter a very defective middle cortex, only here and there are signs of delicate cells which are generally so badly preserved that a wide space seems to separate the outer cortex from the inner cortex which surrounds the vascular cylinder.

Obviously in this problematical organ considerable provision had been made for the conduction of air from the aerial portion of the plant to parts

<sup>1</sup> Henslow, G. "On the Xerophytic Characters of Certain Coal Plants" *Journ. of the Geol. Soc. of London*, 68, 1907.

<sup>2</sup> Weiss, F. E. *Mem. and Proc. Manchester Lit. and Phil. Soc.* 46, 1902.

<sup>3</sup> Weiss, F. E. "The Vascular Branches of Stigmarian Rootlets." *Ann. of Bot.* 16, 1902. *Journ. of Ecology* XIII

rooted in waterlogged soil. But just as in the case of the rootlets, so also in the case of the Stigmarian axis a special type has been described<sup>1</sup> (*Xenophyton radiculosum* of Hick) in which the middle cortex is well preserved, being formed of a much denser mass of cells with no very obvious intercellular spaces. Possibly it bore the rootlets with similar middle cortex mentioned above and it may have belonged to the stem known as *Lepidophloios fuliginosus* which had a similar middle cortex. With this exception the stems of all the *Lepidodendra* and *Sigillariae* have, like the Stigmarian axis, a very defective middle cortex, indicating that this tissue was of a very lacunar nature, as can be seen in the few cases in which it is preserved.

The question now arises how this aerenchymatous tissue communicated with the atmosphere. In the younger stems this took place through the leaves, and a very special feature of the *Lepidodendraceae* are the so-called parichnos strands, passages of lacunar tissue, running from the lacunar middle cortex through the thick-walled outer cortex to the leaves. Normally in the state of preservation found in the so-called "coal-balls," the parichnos strands are mere empty spaces, but occasionally the tissue is preserved and its wider intercellular spaces can be seen. At the base of the leaf the parichnos strand divides into two, the branches running on either side of the vascular bundle, so that when the leaves fall off two distinct marks are found on the leaf-scar by the side of the vascular bundle. No doubt in the leaf the parichnos strands communicate with the lacunar mesophyll and thence through the stomata to the exterior. But when the leaves were shed the two scars, leading into passages filled with a loose-celled tissue, could act in the capacity of lenticels, increasing in size as the massive periderm formation took place in the outer cortex. The stems described formerly as *Syringodendron* are now known to be merely a particular stage in the development of *Sigillaria*, in which the leaf cushions and indeed the scars have disappeared, while the paired parichnos strands are often widely separated and greatly widened, sometimes a centimetre or more in diameter.

Plants with so adequate a provision for the intake of air and for its conduction to the tips of the absorbing organs seem clearly to have required special provision for the aeration of their roots like marsh or aquatic plants, and we may, therefore, consider the *Lepidodendraceae* as such. It is true that the leaves of these plants show some provision for reducing transpiration. Even in the flattened leaves of *Lepidodendron* there are two deep grooves on the under surface into which the stomata open, while in *Sigillaria* the much narrower and almost acicular leaf has deeper grooves and the sclerenchymatous tissue is very well developed. Also the vascular bundle of the leaf is surrounded by a massive sheath of tracheids which would have been able to serve for water storage. We may perhaps explain the xerophytic modifications

<sup>1</sup> Weiss, F. E. "On *Xenophyton*, etc." *Mem. and Proc. Manchester Lit. and Phil. Soc.* 46,

of the leaves of the Lepidodendraceae, as of other marsh plants, by reflecting that the large development of lacunar tissue, which was necessary for the efficient aeration of the roots embedded in a waterlogged soil, would of necessity increase the amount of moisture given off into the wide intercellular spaces. If therefore the leaf were of normal mesophytic type, it would be liable to an excessive amount of transpiration. Hence possibly the tendency for many marsh plants to decrease the size of the leaf. The xerophytic leaf formation of certain aquatic and marsh plants may therefore have been of the nature of a compensation for the large development of intercellular spaces, necessitated by the need for aeration of the roots. The leaves of the Lepidodendraceae, in spite of their xerophytic appearance, may have given off as much water vapour as those of a mesophytic plant with larger leaves but smaller intercellular spaces in stem and root. The general appearance of a leaf does not always give us a correct idea of the amount of transpiration, as has been shown by the work of Prof. Senn<sup>1</sup> and his pupils in connection with alpine plants. Thus he found that the thin leaves of *Alchemilla vulgaris* gave off almost as little water vapour as the succulent leaves of *Sempervivum*, while the thick-leaved *Ranunculus glacialis* and *Homogyne alpina* gave off five or six times as much water vapour as the thin-leaved *Alchemilla*. Experiments carried out in my laboratory have shown that the pendant mature leaves of *Eucalyptus*, generally regarded as xerophytic, transpire as much if not more than the more horizontally expanded and more delicate leaves of the immature plants.

Those who, like Prof. Henslow, maintain that the Lepidodendraceae were not swamp plants but represent the vegetation of drier regions, may suggest, as some have done, that the remains of these plants had been carried into the marshy peat, which subsequently became the coal. Two facts may be brought forward against this view. In the first place, it is well known that in the Lancashire Coal Measures many Stigmarian stumps are rooted in bands of clay, often known as Stigmarian Clay, which lies immediately below the coal seam, and this, no doubt, represents the fine muddy bottom of the swamp in which the vegetable débris accumulated to form a peat. Secondly, in the so-called "coal-balls" which have preserved for us the peaty mass in a petrified condition, we find the ubiquitous Stigmarian rootlets penetrating the entire mass and pushing their way into the decaying tissues of the various plants of which the peat was formed.

To say that all the other plants associated with the water-loving Calamites and Lepidodendra in the coal-balls were aquatic or even marsh plants would be going too far, nor will time permit me to discuss the nature of all the interesting forms. That most interesting and specialised plant, *Sphenophyllum*, would well repay further investigation from the point of view of physiological

<sup>1</sup> Senn, G. "Untersuchungen über die Physiologie der Alpenpflanzen." *Verhand. d. Schweizer naturforsch. Ges.* Bern, 1922.

anatomy, and such investigation might settle the question as to whether it is an aquatic plant or not. I would like, however, to touch upon two groups of plants which certainly require consideration if we are to form any idea of the forest vegetation to which we owe our coal formation. I refer to the Pteridosperms and the Cordaitaceae. Both have leaves which show certain xerophytic adaptations, and neither in their foliar organs nor in the stem have they any large developments of air-conducting tissues such as we have seen in the Calamites and the Lepidodendraceae. It might in their case, therefore, be suggested with a greater degree of probability that fragments of these seed-bearing plants had been carried by wind or water into the peaty mass in which the Equisetales and Lycopodiales grew. That I do not believe to have been the case, for young and delicate roots of *Lyginodendron* are found evidently growing in the peaty mass, and even root tips have been preserved in such perfection that we may assume this plant to have been rooted in the peat. The young roots of *Lyginodendron* too, when well preserved, often show a considerable amount of lacunar tissue<sup>1</sup>. So though it may have had the habit of a scrambling fern, it may have been able to root in marshy ground. For *Cordaites* I think we must assume generally that it was rooted in drier peat; for apart from the absence of aerenchyme and the very considerable development of periderm, we have the fact that the roots sometimes possessed mycorrhizal development<sup>2</sup> which we should associate with drier conditions of the peat rather than a waterlogged condition of the soil, just as we find *Erica* and *Calluna* with mycorrhiza on drier peat. I would picture the marsh, therefore, as possibly formed by the filling in of some large expanse of shallow water in the first place by Calamites, which possessed a rhizomatous development that enabled them to colonise the lagoon from the margin and thus to prepare the ground for subsequent vegetation. The Lepidodendra would probably be confined to the regions nearer the shore, since they do not generally show such indication of progressive growth by vegetative means as do the Calamites. It is true that it has been suggested that the Stigmarian rhizomes may have given rise by budding at intervals to upright stems, but we have little evidence that this was the case. Some curious short conical axes of an uncertain nature have been described by Goldenberg<sup>3</sup>, sometimes with the *Syringodendron* marking, referred to above as probably functioning like the lenticels of the recent trees. Such growths (*Sigillaria cactiformis*), 18 ins. in height, might be compared physiologically, though not morphologically, to the so-called "knees" which surround the stem of the Swamp Cypress (*Taxodium*) and other swamp and mangrove plants.

The gradual accumulation of decaying vegetable matter and the filling in

<sup>1</sup> See Scott, D. H. *Extinct Plants*, Fig. 37. And FELIX, J. *Carbonpflanzen*, Pl. II, fig. 2.

<sup>2</sup> Osborn, T. G. B. "The lateral roots of *Amyelon* and their Mycorrhiza." *Ann. of Bot.* 23, 1909.

<sup>3</sup> Goldenberg, F. *Flora saraepontana fossilis*. Saarbrücken, 1855.



of the expanse of water would prepare the way after a time for plants with less adaptation to a watery medium. To this type belonged probably the *Lepidophloios* referred to above, with little provision in its stem for conduction of air and possibly with the similarly constructed rhizome (*Xenophyton*) and rootlets. Together with *Lepidophloios*, or perhaps in even drier localities, true seed-bearing plants, the Pteridosperms and Cordaitaceae, may have established themselves. Having determined the marsh-like nature of the Coal Measure forest, we have to consider whether it was a salt marsh or a fresh-water marsh. The former view has been advanced by Dr Stopes and D. M. S. Watson<sup>1</sup>. These authors have based their opinion partly on the xerophytic modifications of so many of the Coal Measure plants and partly on the preservative nature of sea-water, which they think accounts for the excellent preservation of many of the tissues found petrified in the coal-balls. It may, however, be pointed out again that xerophytic modifications are quite common in the case of certain plants (*Scirpus*, etc.) growing in fresh-water marshes and that the peculiar succulent modifications of halophytic plants are absent from the plants of the Coal Measures. Nor do we find any of the recent representatives of the Equisetales and Lycopodiales in salt marshes, while on the other hand various species of Equiseta are inhabitants of fresh water and so is *Isoetes*, the nearest living ally of the Lepidodendra. Moreover, as regards the preservation of tissues, humic acid is known to be an excellent preservative of vegetable remains, and though Stopes and Watson point out that the coal-forming mass of vegetation did not correspond to true peat in the sense in which we are accustomed to use the word in relation to moorland peat, it was in all probability "rich in peaty acids." If that were the case we might expect the plant remains to decay very slowly and thus not only provide a coal seam of considerable thickness, but maintain their condition with little alteration until they become petrified, as they were by the infiltration of water charged with lime after the swamp had become covered by the sea, as was probably the case with those seams which have yielded the calcareous concretions known as coal-balls. As indicating the great preservative power of peat formations, Milde<sup>2</sup>, in his monograph of the Equiseta, gives an account of the discovery near Chur in Switzerland of a peat layer about 10 ft. in thickness which had been covered up by mountain debris in apparently prehistoric times and in which remains of the rootstocks of *Equisetum limosum* were so well preserved that they could hardly be distinguished from fresh material. Even the starch grains were preserved in the cells. Other observers too have indicated the excellent preservation of tissues of plant remains embedded in peat.

If brackish at all, these swamps may have derived a slight salinity, like

<sup>1</sup> Stopes, Marie, and Watson, D. M. S. "Distribution and Origin of the Calcareous Concretions in Coal Seams." *Phil. Trans.* 200, 1908.

<sup>2</sup> Milde. *Monographia Equisetorum Nova Acta*, 1867, p. 348.

some of the Norfolk Broads, as shown by Miss Pallis<sup>1</sup>, from the underground salt-water table communicating with the base of the fresh-water marsh. For it is very likely that these swamps occupied the low-lying areas near the coast from which they may have been separated by a system of dunes. In that case a present-day analogy would be the Big Cypress Swamp of South Florida. This is stated to be 200 miles long by 30 broad and though coming near to the coast is separated from the coastal mangrove swamps by low-lying land of the savannah type.

Having discussed the probable edaphic factors of the Coal Measure forest, we must consider the possible climatic conditions under which these palaeozoic plants grew. This point has received some attention from various botanists, Seward's *Fossil Plants as a Test of Climate* being probably the best-known discussion of geological climates from the botanical point of view. Quite recently Gothan<sup>2</sup> has discussed this problem in his *Palaeobiologische Betrachtungen* and the question has also been dealt with by Potonié<sup>3</sup>. The old idea that the climate must have been very moist can no longer be supported in view of the xerophytic character of the foliage of many of the carboniferous plants; on the other hand, the view that the temperature must have been uniformly warm and similar to that of tropical or sub-tropical regions has much to support it. Uniformity of the temperature together with considerable rainfall, such as is found to-day in the tropical belt, is conducive to the growth of trees and to forest formation, and the wood of such trees is characterised by the absence of annual rings, caused by the alternation of seasons in temperate climes. Now one of the most characteristic features of the secondary wood of the Coal Measure plants is the absence of annual rings. It is true that we occasionally get appearances like annual rings both in the wood of *Lepidodendron* and also in *Stigmaria*, but they are in no sense definite annual rings, only spasmodic irregularities in the development of the secondary tissues. Williamson was probably correct in his statement that "the meristematic activity of the cambial layer may have manifested itself irregularly rather than periodically."

The roots of *Cordaites* (*Amyelon*) curiously enough are frequently characterised by darker rings, two or three in number, which have at first sight the appearance of annual rings, but they show no such typical alternation of larger and smaller tracheids as one finds in *Pinus* for example. Since *Cordaites* possibly grew as I have indicated above in somewhat drier areas of the peat it is possible that occasional occurrence of drought may be responsible for these markings.

Another objection which has been raised to the assumption of a tropical climate for the development of the Coal Measure swamps has been the sup-

<sup>1</sup> Pallis, M. "On the Cause of the Salinity of the Broads of the River Thurne." *Geograph. Journal*, 1911.

<sup>2</sup> Gothan, W. *Palaeobiologische Betrachtungen über die fossile Pflanzenwelt*. Berlin, 1924.

<sup>3</sup> Potonié, H. *Die Entstehung der Steinkohle*, 1910.

position that the thick mass of decaying peat-like vegetable matter could not accumulate under tropical conditions, as the high temperature would promote a very rapid decay of the vegetable débris. It was pointed out that peat formation requires cool and moist conditions. Of late years, however, quite a number of characteristic tropical swamps with peat or peat-like formation have been described.

Potonié<sup>1</sup>, who has long upheld the tropical nature of the coal forests, has drawn special attention to the discovery by Koorders of a tropical fresh-water swamp in Sumatra (a Sumpf-Flachmoor) which produced a layer of peaty material 9 m. in thickness. This peat, which was of good burning capacity, consisted mainly of the leaves of the trees growing in the swamp, for it was of the nature of a swamp forest. It was of large size, some 12 km. across, and consisted of tall trees 60 or more feet in height and belonging to various Dicotyledonous families. There were few Monocotyledons and no Gymnosperms. This formation seemed to have no connection with or resemblance to the mangrove formation except in the development of breathing roots. There was an almost complete absence of Gramineae and Cyperaceae. Indeed there was practically no ground flora; the soil was covered with rotting leaves through which the pneumatophores projected. There were very few water plants in the stagnant pools. Neither *Sphagnum* nor other mosses were present and there were few Liverworts, Lichens or Ferns.

Since then Keilhack<sup>2</sup> has described the existence of tropical and sub-tropical peat formation in Ceylon. The latter he found in the highlands of the island due to the partial filling up of Lake Gregory. But on the coastland of the island near Ambalangoda behind a sandy belt of dunes he found a peat formation of more tropical character. Here rainfall was about 225 cm. per annum, the mean temperature 28° C., and the peat had accumulated to the depth of 3 ft. Under these conditions the marsh or swamp produced such tree-like forms as *Barringtonia* and *Bruguiera gymnorhiza* though the bulk of the vegetation consisted of Gramineae and Cyperaceae, *Typha* and *Eriocaulon*, with ferns such as *Gleichenia*, *Dryopteris*, *Nephrolepis* and *Acrostichum aureum*. There was a complete absence of mosses. This formation would resemble somewhat the semi-mangrove formation described by Tansley and Fritsch in *The Flora of the Ceylon Littoral*<sup>3</sup>.

The most recent description of tropical swamps from the African continent we owe to Krenkel<sup>4</sup>. He has described a swamp on one of the bays of Lake

<sup>1</sup> Potonié, H. "Die Tropen-Sumpfflachmoor Natur des productiven Carbons." *Jahrb. d. Königl. preuss. Geol. Landesanstalt*, 30, 1909.

<sup>2</sup> Keilhack, K. "Über tropische und subtropische Torfmoore auf der Insel Ceylon." *Jahrb. d. Königl. preuss. Geol. Landesanstalt*, 36, 1915.

<sup>3</sup> Tansley, A. G. and Fritsch, F. E. "The Flora of the Ceylon Littoral." *New Phytol.* 4, 1905.

<sup>4</sup> Krenkel, E. "Moorbildungen im tropischen Africa." *Centralbl. für Mineral. Geol. und Palaeontologie*, 1920.

Tanganyika, near Kigoma, and in a former bay now cut off from the lake. In both cases the filling in has taken place largely by growth of *Papyrus*, but in spite of the tropical conditions a thick layer of peat had been developed. The peat was about 3 ft. in thickness and consisted of a fine mass mostly of root fibres but mixed with some remains of leaves and stems. The rainfall here is about 109 cm. per annum and the mean temperature 22.8° C.

There is no doubt, therefore, that tropical and subtropical climates can produce considerable formations of peaty material and it is no longer necessary to consider that the substantial deposits of vegetable débris which have been transformed into our coals indicate a temperate climate for these palaeozoic plant associations.

The other difficulty which requires to be removed, is how to account for a tropical climate in Britain and in Central Europe, two of the important centres of the formation of palaeozoic coal. Here we have to take into consideration certain geological data such as the fact that during carboniferous times a considerable glaciation occurred over South Africa, South America and Western Australia (permo-carboniferous glaciation). Koppen and Wegener in their recent book<sup>1</sup> suggest that the only way in which it is possible to explain this fact is by supposing the poles to have occupied a different position in that past geological period from the present day position. According to these authors, the South Pole during permo-carboniferous times would have been somewhere to the east of South Africa, and as, according to Wegener, the South American and Australian continents were connected with South Africa, the glaciation of all these areas would be explained. Now supposing the South Pole were in this position and the North Pole in the northern Pacific, the Equator would have run through Mexico, the eastern states of North America, Central Europe, and northern China, along which line palaeozoic coal is found. This equatorial line would in those days have produced a tropical forest vegetation due to high temperature and abundant rainfall, just as occurs now in the tropical belt. This theory, which is based on geological evidence, would therefore be in agreement with the botanical considerations (absence of annual rings, luxuriant growth, etc.) which leads us to suppose that the palaeozoic plants of the Coal Measures lived under tropical conditions. There seems no objection therefore to our concluding from the anatomy of the Coal Measure plants, that they were members of a tropical swamp forest. In all probability this was a fresh-water swamp. The lower forms of vegetable life, the spore-bearing Calamites and Lepidodendraceae were specially adapted to root under water, while the more highly developed forms, particularly the seed-bearing members (Pteridosperms and Cordaitales), were less aquatic and perhaps normally rooted in drier peat. Most of the plants, whether aquatic or terrestrial, were considerably modified for drought resistance, which might indicate a high percentage of humic acid

<sup>1</sup> Koppen, W. and Wegener, A. *Die Klimate der geologischen Vorzeit*, 1924.

in the substratum and also a certain degree of dryness of the atmosphere at any rate at certain periods, either of the day or the year.

But though I venture to put forward these conclusions based on a study of the anatomy of our Coal Measure plants, and though they are in the main in agreement with the views of other palaeobotanists, I would like to emphasise that there are features connected with many of these plants which call for further investigation, and I would emphasise Scott's remarks with which I commenced my address that these plants still offer a wide and promising field of research from the point of view of their physiological anatomy.

# THE VEGETATION OF THE FOREST OF WYRE: A PRELIMINARY ACCOUNT<sup>1</sup>

By E. J. SALISBURY.

WYRE FOREST, on the borders of Worcestershire and Shropshire, is one of the larger areas of natural woodland still remaining in Britain. But, though it is still possible to traverse over five miles of almost continuous woodland from Dowles, on the east, to Cleobury Mortimer, on the west, or nearly five miles of woodland from Coppice-gate, on the north, to Burnt Wood, on the south, yet this large tract is a mere remnant of its former extent. The Forest of Wyre is indeed but a fragment of that large forest area which even in Roman times gave its name to the military settlement on the south of the forest (Wyre-ceastre, the modern Worcester). There is considerable probability that within historic times the area now designated Wyre Forest or the Forest of Bewdley was almost, if not actually, continuous with the great forests of Ombersley and Malvern on the south, Morfe on the north-east (also called the Forest of Bridgenorth), Kinver on the east and Clee Forest on the west. In making this statement the fact has not been ignored that these were forest areas in the purely legal sense which only implied an area of waste land in which the right to hunt was reserved to the Crown<sup>2</sup>. That all of these areas were however forests also in the modern usage of the word is shown by numerous presentments, Court Rolls and other similar documents. The wooded nature of the surrounding country in times past is indicated even at the present day by a number of small scattered woodlands and a few large ones. Of these latter Ribbesford Woods on the west bank of the Severn south of Bewdley, Eyemore and Arley Woods to the north-east of that town, and the woods adjacent to Kinlet Park belong properly to the Wyre Forest itself. In the reign of Henry III the portion of Wyre Forest in Worcestershire alone, was about four miles in breadth<sup>3</sup>, and a survey of 1608 states that the part known as Bewdley Park contained 4142 timber trees of which considerably more than half were more or less decayed. In the adjoining area of Morfe, Ranulf Earl of Chester sold no less than 1700 *Oak* trees between the years 1216 and 1223<sup>4</sup>. This number of large trees is small having regard to the probable area involved, but there is documentary evidence that even at this date much of the oakwood in this area was treated as coppice: thus the survey cited above gives Fecken-

<sup>1</sup> The substance of this account was communicated to the meeting of the British Ecological Society at Birmingham, December, 1923, on the occasion of a visit to the Forest.

<sup>2</sup> Cf. Cox. *Royal Forests*, 2.

<sup>3</sup> Cf. *Victoria County History of Worcestershire*, 2, 318.

<sup>4</sup> Cf. Eyton. *Antiquities of Shropshire*, 4, 215.

ham and Wyre Forests as containing 38,400 timber trees and 1050 acres of coppice<sup>1</sup>.

The causes of the rapid destruction of timber up to the present day are not far to seek. Coal as a fuel was not used to any extent for commerce until about 1700, but from quite early times brine was evaporated at Droitwich, where the salt pans consumed some 6000 loads of wood per annum<sup>2</sup> and large quantities were also consumed by the iron smelting in the Stourbridge district.

The present wooded area occupies high ground sloping towards the Severn on the west and traversed by the deep valley of Dowles Brook separating the Worcestershire and Shropshire portions. The ground rises steeply on either side of Dowles Brook, attaining an altitude of over 400 feet on the north and over 500 feet on the southern limit near Callow Hill.

Geologically practically the whole of this area is situated on the Middle Coal Measures consisting of sandstones, shales and ironstones with sweet coals<sup>3</sup>. Towards the northern edge near Button Oak there occurs a narrow band of *Spirorbis* limestone and further north a small area of woodland occupies soil of Upper Coal Measure origin. The detached areas near Cleobury Mortimer<sup>4</sup>, Ribbesford Woods and Egmore Wood, are all on the Coal Measures, the last named with *Spirorbis* limestone.

This brief description shows that the wooded area occupies for the most part comparatively steep valley slopes on a soil derived almost entirely from non-calcareous rocks. Such is the typical habitat of *Quercus sessiliflora* in this country and it is therefore hardly surprising that over almost the whole of this area *Q. sessiliflora* is not only the dominant tree but is often present in almost pure stands.

Several areas, such as Mowley Wood near Cleobury Mortimer, parts of Ribbesford Wood and Chamberline Wood, are high forest, but for the most part the woods are coppiced on the compartment system with approximately a 16-18 years' rotation. Each area is clear cut except for a few seeding trees. In the high forest measurements showed the distance between standards to vary from 15 to 70 feet.

The following measurements of trees whose age was estimated from the number of annual rings, shows the rate of growth to be somewhat more rapid than is usual on a good site, and further emphasises the suitability of the habitat for *Q. sessiliflora*. According to Schlich<sup>5</sup> the mean diameter of oak at 90 years in a first class location is just over 14 inches, whilst at 30 years the diameter is just under 4½ inches. Other types of forest treatment are also met with in which there are two ages of coppice, the general matrix being on

<sup>1</sup> Cf. *Victoria History*, 318. "

<sup>2</sup> Cf. *Victoria History of Worcestershire*, 258.

<sup>3</sup> Cf. T. C. Cantrill. *A Contribution to the Geology of the Wyre Forest Coalfield*. Kidderminster, 1895.

<sup>4</sup> This wood in times past supported 500 swine. Cf. *Eyton*, 4, 193.

<sup>5</sup> *Manual of Forestry*, 3, 344.

a shorter rotation than the more sparsely scattered oaks treated on a long rotation. The larger coppice stems are used for pit props, the smaller cordwood (1-4 inches) for the large industry in charcoal, and some of the smaller branches suitable for rent-oak are the raw material for oak baskets.

Diameter (in.)	Age (yrs)	Average increase per year (in.)
2	16	0.125
5 - 5½	32	0.164
7½-11	34	0.272
20	85	0.235

This mode of treatment of the oak as coppice has a marked effect on the character of the vegetation and almost certainly retards the natural edaphic succession, besides presenting different phases in the ebb and flow of marginal species which comprise so large a part of the flora of newly coppiced areas<sup>1</sup>.

The soil of Wyre Forest presents a thickness of raw humus varying according to the lapse of time since the last "cut." For example, in a recently cut area (*ca.* 3 years) there was practically no litter and the soil was about 30 per cent. bare. In another area with 7 years' growth the raw humus had an average thickness of about an inch, whilst the humus layer under stands of 16 to 19 years' growth, varied from a fraction of an inch to over 2 inches. The underlying soil is mostly sandy or sand followed by a sandy clay resting on rock at a depth often not exceeding 2 to 3 feet.

Soil analyses show that there is for the most part a very low calcium content and the reaction of the surface soil is generally markedly acid. At the edges of streams, however, the reaction may even be slightly alkaline, and by Dowles Brook and some of its tributary rivulets calcareous tufa occurs. The slope of Seckley Wood leading down to the Severn is occupied by beechwood, which Lees, writing nearly half a century ago<sup>2</sup>, regarded, and probably rightly, as planted. Nevertheless, we find here a relatively high proportion of calcium and a type of vegetation containing species characteristic of calcareous soils.

Wyre Forest, from its situation on a mass of nearly uniform rock subsoil, affords an opportunity of studying the differentiating action of the progressive leaching of the soil (the rainfall is about 25 inches per annum), whereby the higher parts have become extremely poor in bases, especially calcium, and present an acid reaction; whilst the lower slopes, towards Dowles Brook and the Severn, are enriched by the salts leached from above and present soils which are relatively mild in reaction with a more basic type of flora. This is illustrated alike by the tree, shrub and herbaceous vegetation.

Although *Q. sessiliflora* is the only oak on the higher parts of the forest *Q. robur* (and *Q. robur* × *Q. sessiliflora*) is found towards the foot of the slopes and on the alluvial flats. Here too occur *Ulmus montana*, *Prunus avium*,

<sup>1</sup> Cf. *Salisbury*. This JOURNAL, 4, p. 112 and 6, p. 40.

<sup>2</sup> *Aspects of Nature*.



*Fraxinus excelsior*, *Populus tremula* and *Alnus glutinosa*, of which the first three are particularly associated with non-acid soils.

Apart from *Q. sessiliflora* the only common tree is *Betula alba*. *Ilex aquifolium*, *Pyrus aucuparia* and *P. torminalis* are all occasionally present and sometimes locally frequent, whilst a striking feature, as in so many of our western *Q. sessiliflora* woods<sup>1</sup>, is the presence of sparsely scattered trees of *Taxus baccata*.

The shrubs and undershrubs also show a relation to the difference in the soil on the slopes fed by percolation water from above. In the higher parts *Vaccinium myrtillus* is often abundant, whilst other "calcifuge" species present are *Calluna vulgaris*, *Erica cinerea*, *Ulex minor* and *Sarothamnus scoparius*. By contrast, *Corylus avellana*, though by no means absent above, becomes frequent on the lower slopes and here also occur *Sambucus nigra*, *Euonymus europaeus*, *Ligustrum vulgare*, *Rhamnus catharticus* and even *Clematis vitalba*.

The generally "calcifuge" character of the main body of Wyre Forest is sufficiently indicated in the herbaceous flora by the abundance of *Digitalis* (and *Calluna* seedlings) after coppicing and also the frequency of *Holcus mollis*, *Hypericum pulchrum*, *Solidago-virgaurea*, *Pyrola* spp., *Luzula pilosa*, *Aira flexuosa*, *Triodia decumbens*, *Pteridium aquilinum* and *Blechnum spicant*.

The following species characteristic of the foot of the slopes sufficiently illustrate the contrast.

*Arum maculatum* (f.c.), *Allium ursinum*, *Adoxa moschatellina* (l.), *Ajuga reptans*, *Astragalus glycyphyllos* (r.), *Asperula odorata*, *Circaea lutetiana* (f.c.), *Campanula trachelium* (r.), *Ficaria verna* (f.—f.c.), *Galeobdolon luteum* (o.—f.), *Galium cruciatum* (r.r.), *Geum urbanum*, *Lathraea squamaria* (r.), *Mercurialis perennis* (c.—a.b.), *Millium effusum*, *Melica nutans* (l.), *Nepeta glechoma*, *Paris quadrifolia*, *Pimpinella major*, *Ranunculus auricomus* (r.), *Scilla nutans* (f.), and *Sanicula europaea*.

In addition the following "calcicole" species have been recorded from Wyre: *Vicia sylvatica*, *Geranium sanguineum*, *Inula conyza*, *Carlina vulgaris*, *Chlora perfoliata*, *Gentiana amarella*, *G. campestris*, *Spiranthes autumnalis*, etc. It may perhaps be evidence of continued leaching that some of these appear to be less common than formerly.

The herbaceous vegetation of an alluvial flat bordering the north bank of Dowles Brook, which was examined by Mr Tansley and the writer, is essentially that of a *Quercus robur* wood and *Q. sessiliflora* wood combined, and indeed both species of oak are there met with.

The comparatively low rainfall, the steepness of the slopes and the sandy character of the subsoil combine to produce a very dry soil which is reflected in the poverty of the flora over large areas. The comparative richness, both in species and individuals, of the lower slopes and alluvial flats as compared

<sup>1</sup> Cf. Salisbury and Tansley. This JOURNAL, 9, p. 34 and Pl. II.

with the crests of the ridges, is probably largely determined by the difference in water content. But the absence of calcicole species from the higher parts of the forest, species which normally flourish in dry locations, indicates that reaction is an important factor in influencing their distribution. The humidity factor may be responsible for the much greater frequency of *Frullania dilatata* and *F. tamarisci* on the trunks in the valley.

The density of the ground flora is largely determined by the phase in the coppicing rotation as it affects the light intensity. Determinations showed that during the *light phase* of a recently-cut area the intensity might be 73 per cent. or over at the ground level. In 16-year-old coppice this was reduced to from 50–66 per cent., whilst in old high coppice the light intensity was only 35 per cent. or even less, and the ground flora very sparse, even with respect to prevernal species.

In parts of Ribbesford Wood under high forest, where the light intensity is low and the water content moderately high, a mossy vegetation occurs, recalling that characteristic of many *Quercus sessiliflora* woods in North Wales (dominant mosses: *Dicranum scoparium*, *Mnium hornum*, *Polytrichum formosum*, *Hypnum cupressiforme*).

*Luzula maxima* occurs as a local dominant in its characteristic situation on the "flush" slopes above the Severn.

It is in agreement with the generally acid character of the soil that the molluscan fauna of the wood floor is very poor. On the other hand, the cryptogamic flora, with respect to the higher fungi, the mosses and the liverworts, is rich.

The following liverworts occur and are characteristic of *Quercus sessiliflora* woods in general: *Aplozia crenulata* (var. *gracillium*) (c.), *Cephalozia bicuspidata* (f.), *Calypogeia trichomanis* (f.), *C. fissa* (o.), *C. arguta* (r.), *Diplophyllum albicans* (c.), *Fossombronina pusilla*, *Lepidozia reptans*, *Lejeunea cavifolia* (r.), *Lophozia ventricosa*, *Lophocolea bidentata* (c.), *L. cuspidata*, *L. heterophylla*, *Nardia scalaris*, *Plagiochila asplenoides* (c.), *Scapania nemorosa* (f.), *Trichocolea tomentella* (l.). A striking feature of the hepatic flora is that several species usually associated with the subalpine region have been recorded from Wyre Forest, though of rare occurrence there<sup>1</sup>. These include: *Marsupella emarginata*, *Aplozia riparia*, *Plagiochila spinulosa*, *Lophozia quinquedentata* and *Blepharostoma trichophyllum*. *Madotheca platyphylla*, a species especially frequent on calcareous soils, is not uncommon in the valleys. The rare occurrence of *Bazzania trilobata* is of interest, as this species is often a striking feature in upland *Quercus sessiliflora* woods.

One of the most striking features of the Wyre Forest, and especially well shown also in Ribbesford Woods, are the numerous old "hearths" where charcoal has been burnt.

These "hearths" are of all ages from blackened areas devoid of vegetation

<sup>1</sup> Cf. Amphlett and Rea. *Flora of Worcestershire*.

through a succession of phases culminating in a thicket of shrubs and trees. It is especially on these areas that seedling trees develop, a fact to which attention has been already called and which can be correlated with the alteration in the character of the surface soil.

Examination of soil samples taken from a one-year-old hearth showed a slightly alkaline reaction, the average hydrogen-ion concentration being pH 7.2. The total carbonates averaged 0.35 per cent. and the soil gave a marked nitrate reaction.

The soil just around this hearth (sampled to the same depth—0.3 inches) showed a slightly acid reaction (pH 6.1) and the carbonate content was only 0.10 per cent. Also the nitrate reaction was slight. A second hearth, judged to be about two years old, was slightly acid in reaction (pH 6.1), whilst the surrounding soil was markedly acid (pH 5.6). The total carbonates in the hearth soil ranged from 0.12 to 0.19 per cent., but the surrounding soil yielded only 0.01 per cent. or under. This hearth, moreover, showed a marked nitrate reaction, whilst the soil of the wood around gave practically no such reaction.

A similar relation was found to obtain between the soil of the hearth and the surrounding woodland in samples from Haye Wood, near Ludlow, and Haugh Wood, south of Hereford.

The conditions then on an old hearth are probably favourable in several respects, namely:

- (a) Absence of competition.
- (b) Lowered acidity.
- (c) Increased carbonates.
- (d) Increased nitrates.

Similar advantages may accrue from coppicing<sup>1</sup>, which also frequently results in the production of areas suitable for colonisation. But though the relief from competition pressure may be as great as on a hearth the edaphic changes are not nearly so marked and it is therefore significant of adverse edaphic factors that regeneration on old hearths is much more marked than on coppiced areas.

The early stages in colonisation of a hearth are frequently marked by an extraordinary profusion of *Marchantia polymorpha*, *Funaria hygrometrica*, *Ceratodon purpureum* and sometimes *Holcus lanatus*. Other species of frequent occurrence are *Cardamine hirsuta*, *Cerastium triviale*, *Epilobium angustifolium*, *Fragaria vesca*, *Hypericum humifusum*, *Luzula pilosa*, *Myosotis arvensis*, *Prunella vulgaris*, *Sagina procumbens* and *Veronica serpyllifolia*.

In older phases *Betula* seedlings are sometimes abundant and oak and willow seedlings occur, together with an increasing number of woodland plants. But the more calcicole character of the hearth vegetation is evident, even in old examples where *Sanicula europaea* and similar species may occur, though absent from the surrounding vegetation.

<sup>1</sup> Cf. Salisbury. This JOURNAL, 6, p. 40.

In the coppiced areas *Pteridium aquilinum* and *Holcus mollis* sometimes share dominance, but other species which are often very common or even abundant are *Aira flexuosa*, *Calluna vulgaris* (seedlings), *Digitalis purpurea*, *Galium saxatile*, *Hypericum pulchrum*, *Luzula pilosa*, *Rubus fruticosus* agg., *Vaccinium myrtillus* and *Veronica officinalis*. In coppiced areas towards the base of the valleys, however, *Lychnis dioica* and *Galeobdolon luteum* may become conspicuous as in *Quercus robur* woods.

Mosses are often conspicuous features of the recently-cut areas, notably *Catharina undulata*, *Dicranum scoparium*, *Hypnum cupressiforme*, *Mnium hornum* and *Polytrichum formosum*.

The headwaters of the smaller streams present a "flush" vegetation in which *Ranunculus repens*, *Lysimachia nemorum*, *Cardamine flexuosa*, *Ajuga reptans*, *Circaea lutetiana*, *Chrysosplenium oppositifolium*, *Lychnis dioica*, *Nepeta glechoma*, *Ulmaria palustris*, *Veronica montana*, *Allium ursinum* and *Carex pendula* are all of common occurrence. The last named in particular recalls the flush society as met with in the *Quercus sessiliflora* woods on the May Hill Sandstone of the Malvern area and is indeed a feature of this type of woodland.

It has often been stated that *Q. sessiliflora* is less subject to the depredations of *Tortrix viridiana* than its congener owing to the slightly earlier development of the leaves in *Q. robur*. Though probably true in the main it may be noted that in 1918 *Q. sessiliflora* in Wyre Forest was badly attacked by the larvae of this moth.

The appended list of trees, shrubs and undershrubs, though probably not complete, gives a general idea of the composition of the upper layers of the vegetation.

#### List of Trees, Shrubs and Undershrubs recorded from Wyre Forest.

<i>Acer campestre</i> (in valley).	<i>Fraxinus excelsior</i> (l. especially in valleys).
„ <i>pseudo-platanus</i> (l. sub-spontaneous).	<i>Hedera helix</i> (r.—l.f.).
<i>Alnus glutinosa</i> (l.f. by streams).	<i>Ilex aquifolium</i> (o.—l.f.). [Often killed by deer and rabbits.]
<i>Betula alba</i> (f.—l.ab.). [The abundance of this species and the rarity if not complete absence of true <i>B. pubescens</i> recalls the conditions in the May Hill Sandstone woods of the Malvern area <sup>1</sup> .]	<i>Juniperus communis</i> (r.).
<i>Calluna vulgaris</i> (r.—l.ab.).	<i>Ligustrum vulgare</i> (o. in valley).
<i>Clematis vitalba</i> (l. near Dowles Brook).	<i>Lonicera periclymenum</i> (f.c.—r.r.).
<i>Corylus avellana</i> (r.—f. especially on valley slopes).	<i>Populus tremula</i> (r.).
<i>Crataegus monogyna</i> (f.).	<i>Prunus avium</i> (r.—l.f.).
„ <i>oxyanthoides</i> .	„ <i>cerasus</i> .
<i>Erica cinerea</i> .	„ <i>domestica</i> .
„ <i>tetralix</i> .	„ <i>insititia</i> .
<i>Euonymus europaeus</i> (valleys r.r.).	„ <i>spinosa</i> .
<i>Fagus sylvatica</i> (l.).	<i>Pyrus communis</i> .
	„ <i>malus</i> (var. <i>acerba</i> and <i>mitis</i> ) (r.r.—l.f.).
	<i>Quercus robur</i> (in valleys).
	„ <i>sessiliflora</i> (ab.) and hybrids in valleys.
	<i>Rhamnus catharticus</i> .

<sup>1</sup> Cf. Salisbury and Tansley, l.c.

*Rhamnus frangula* (l.c.—r.r.).

*Rubus fruticosus* agg. (o.—v.c.). The following segregates have been recorded: *R. suberectus*, *villicaulis*, *pubescens*, *macrophyllus*, *pyramidalis*, *Babingtonii*, *ericetorum*, *Bloxamii*, *longithyriger*, *foliosus*, *rosaceus*, *dasyphyllus*, *Bellardii*, *hirtus*, *caesioides*.

*Rubus saxatilis*.

*Salix aurita*.

„ *caprea* (r.).

„ *cinerea*.<sup>1</sup>

*Sorothamnus scoparius* (o.).

*Sorbus aria* (v.r.).

„ *aucuparia* (o.).

„ *torminalis*.

*Tilia parvifolia* (r.).

*Taxus baccata* (r.—l.f.).

*Ulex gallii* (o.—l.f.).

„ *minor* (r.).

*Ulmus montana* (l.f.) in valleys.

*Vaccinium myrtillus* (f.—o.).

*Viburnum opulus*.

# NOTE ON THE EDAPHIC SUCCESSION IN SOME DUNE SOILS WITH SPECIAL REFERENCE TO THE TIME FACTOR

By E. J. SALISBURY.

(With two Figures in the Text.)

FROM the examination of a large number of samples from successive dune ridges on Blakeney Point the writer was able to demonstrate, (a) the progressive leaching of the carbonates with increasing age, (b) the passage from an alkaline to an acid condition, and (c) the progressive increase in the organic content. It was moreover shown that these changes were accompanied by changes in the flora which, broadly, consisted in diminution of calcicole species and the advent of calcifuge types<sup>1</sup>. In the Blakeney area the age of the successive dune ridges can only be inferred (except in the case of the youngest) from their relative position and it seemed therefore desirable to find some dune area where the respective ages of the dune ridges could be ascertained with a reasonable degree of accuracy. For this purpose a visit was made to the Southport dune system.

The ages of the ridges in this dune system have been assessed partly by the examination of old maps (e.g. Speed's map of 1610, the Bold Estate map of 1736) and descriptions. In this way it has been possible to fix the approximate age of certain points and to establish the average rate of advance of the dunes on this coast. Secondly, the very early arrival of *Salix repens* in the hollows between the dune ridges makes it possible to utilise the number of annual rings in the thickest and oldest axes as a check on the estimates. In connection with the documental evidence I would record my indebtedness to the Public Library officials of Southport, whose help was ungrudgingly placed at my disposal, and to the authorities of the British Museum Library, also to W. Ashton's admirable book, *The Evolution of a Coastline*.

The area chiefly examined was the dune series extending from Mad Wharf to Formby Golf Links and Freshfield.

The youngest ridge (a) on the sea face consisted of embryo dunes scarcely coalesced, and colonised by *Triticum junceum* and *Psamma* (*Ammophila*) *arenaria*. The latter appears to be the later arrival, as is to be expected from its less halophytic characteristics. This ridge was estimated to be about two years old.

<sup>1</sup> Cf. Salisbury, E. J. "The Soils of Blakeney Point: A study of soil reaction and succession in relation to the plant covering." *Ann. Bot.* 36, pp. 391-431, 1922.

The second ridge (b) was slightly higher than the first and bore an almost pure growth of very dense and vigorous *Psamma*. The crest was about 32 yds. distant from ridge (a) and probably represented a formation of about four years earlier.

The ridge (c) was probably about 14 years old, and though *Psamma* is abundant it is clearly not so vigorous as on ridge (b). Other species were now conspicuous, notably *Festuca arenaria*, *Cirsium arvense*, *C. lanceolatum*, *Senecio jacobaea*, *Euphorbia paralias* and *Carlina vulgaris*. The last is quite frequent, and its presence in this early stage is noteworthy in view of its calcicole tendency and the high calcium content of the early dune phases.

Between this ridge and the ridge (b) there is an interval of about 57 yds. in which is a very narrow "slack" occupied by *Salix repens*, but with a considerable amount of bare ground between, and evidently in an early stage of colonisation, perhaps representing about three years' growth.

Ridge (d), about 25 years old, was separated from (c) by a well-developed "slack" in which the very common *Salix repens* is accompanied by *Parnassia palustris* (c.), *Pyrola rotundifolia* var. *arenaria*, *Glaux maritima* (v.c.), *Sagina nodosa*, *Carex arenaria*, *C. oederi*, *Hydrocotyle vulgaris*, *Ranunculus flammula*, *Juncus lamprocarpus*, *Eleocharis palustris*, *Euphrasia nemorosa* and *Mentha aquatica*. The ridge itself bore abundant *Psamma*, but somewhat unhealthy in appearance. Here one noted the much greater frequency of the Carlina Thistle and in addition to the species of ridge (c), *Rumex crispus* var. *trigranulatus*, *Euphorbia portlandica*, *Cynoglossum vulgare*, *Viola canina*, *Lotus corniculatus*, *Leontodon autumnalis* and *Hieracium umbellatum*.

Ridge (e) is the highest dune ridge and is probably about 55 years old. *Psamma* is still abundant but more unhealthy in appearance than on ridge (d). Additional species encountered in this stage were *Rubus caesius* (l.a.), *Ononis repens*, *Sedum acre*, *Luzula* sp., and numerous plants of *Chlora perfoliata*.

In the older slacks, particularly near their margins, several usually calcicole species occur with some frequency, notably *Gentiana campestris*, *G. amarella*, *Linum catharticum* and *Chlora perfoliata*. Still more striking is the fact that in addition to the common *Epipactis palustris* several orchids occur in these wet slacks, such as *Spiranthes autumnalis*, *Orchis pyramidalis*, etc., which we elsewhere associate more particularly with dry chalky pastures.

The oldest dune phases are mere remnants in the neighbourhood of Freshfield and Cloven-Ley-Dale, which, though serving for soil comparison, occupy too small an area to permit of a typical vegetation being developed upon them. Most of the older dunes have been taken into cultivation or otherwise interfered with by man. On some of these remnants however *Calluna* has developed, witnessing to the calcifuge trend of the succession. It is estimated that the *Calluna* patch examined represented a dune formed about 280 years ago. The planting up of the dunes with pines has to some extent interfered with the succession from ridge (d') to the oldest phases. A study of the table

TABLE I. Analysis of dune soils, Southport.

Dune ridge	Approximate age yrs.	Hydrogen-ion concentration		Carbonate content		Loss on ignition %	
		pH	pH	% (as $\text{CaCO}_3$ )		corrected for $\text{CO}_2$	
(a) ... ..	2	8.2	5.6	-6.7	Av. 6.3	0.126-0.762	Av. 0.528
(b) ... ..	6	8.2	3.6	-4.5	Av. 4.15	0.18 -0.492	Av. 0.335
(c) ... ..	14	8.15	2.2	-3.54	Av. 3.17	0.67 -0.70	Av. 0.68
(d) ... ..	25	7.8	1.9	-2.5	Av. 2.35	0.314-1.09	Av. 0.70
(d') ... ..	29	7.6	2.72	-3.5	Av. 3.10	0.53 -0.74	Av. 0.63
(e) ... ..	55	7.8	2.1	-3.2	Av. 2.5	0.81 -0.95	Av. 0.88
(f) ... ..	100	7.2			Av. 1.14	3.60 -4.50	Av. 4.00
(g) Nr. Cloven-Ley-Dale	200	6.4			Av. 0.2	2.2 -3.2	Av. 2.70
(h) Nr. Freshfield	270	6.8	0.04	-1.0	Av. 0.33	2.79 -3.06	Av. 2.92
(i) Nr. West Lane	280	6.8	0.14	-1.2	Av. 0.50	2.83 -2.90	Av. 2.86
(j) Heather Dune	280	5.5	0.03	-0.19	Av. 0.09	4.4 -25.7	Av. 15.0

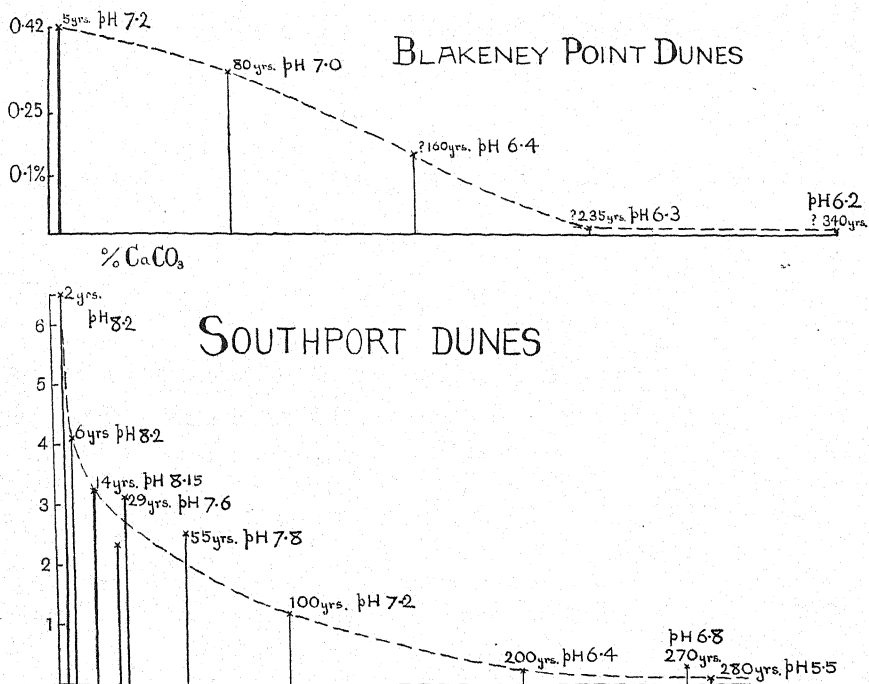


FIG. 1. Rate of leaching of calcium carbonate from dunes.

will however show that, except for ridge (d') and the dune near Cloven-Ley-Dale, there is with the progress of time an increase in the hydrogen-ion concentration. At first appreciably alkaline, the dune soil becomes neutral after the lapse of something over a hundred years and, after the passage of another century, the soil has become appreciably acid. The dune at Cloven-Ley-Dale still bore very sparse *Psamma arenaria*, though clearly very unhealthy and probably on the verge of extinction; it is therefore not perhaps without



significance that the pH value, viz. 6.4, is only slightly less acid than locations at Blakeney Point (pH 6.1-6.2), where also the Marram grass appears to be only just persisting. The dunes at Freshfield and near West Lane are both used more or less as meadow-land and this slight amount of human interference probably accounts for their reaction being rather less acid than might be expected from their age. The *Calluna* dune, though only a remnant, has been obviously left untouched and the reaction here corresponds with the highest acidity realised on the Blakeney Dunes (cf. *l.c.* p. 424).

The average carbonate content shows a continual decrease with age (Fig. 1), except for these same dunes (*d'*), (*h*) and (*i*). The early phases have a content of calcium carbonate, that is, over fourteen times that of the embryo dunes at Blakeney (0.425 per cent.), but in comparing the rate of leaching in the two areas the much lower rainfall on the east coast as compared with the west must be taken into consideration. In both areas the rate of leaching is at first rapid and then falls off as the amount of carbonate rather than the amount of rainfall becomes the limiting factor. The number of years that the main ridge at Blakeney has been subjected to leaching is probably about 80, and in this interval of time the surface soil would appear to have lost about 20 per cent. of its carbonate content. Comparing the undisturbed dunes (*g*) and (*j*) of the Southport system, we find a loss in the same interval of time of 55 per cent., starting with about half the carbonate content. If now we compare (*c*) and (*f*), giving a similar interval of years but starting with a very much higher content, the percentage loss is 64. The rate of leaching in the early stages will clearly be influenced by a number of factors of which by no means the least important is the nature of the comminuted shell fragments. If the carbonate content depends on the presence of few large fragments the surface will be small in comparison with the volume, and the rate of leaching will be slow, but if the same volume be represented by numerous small fragments the rate of leaching will be rapid. Even if the particles were spherical the diminution in surface as leaching proceeds would of course be proportionately much less than the diminution in the volume, but many of the particles are flattened so that whereas the volume of carbonate diminishes rapidly the surface acted upon undergoes but little change. Whilst the number of samples obtained from each age of dune do not warrant the assumption of a high degree of accuracy, yet it is significant in this connection that the *mean annual percentage loss* calculated for the later periods shown below are of the same order of magnitude.

	Period yrs.	Mean annual loss %
(a)-(b)	2- 6	8.5
(b)-(c)	6- 14	2.95
(c)-(d)	14- 25	5.74
(d)-(f)	25-100	0.68
(f)-(g)	100-200	0.82
(g)-(j)	200-280	0.68

6-100 yrs., 0.72 %

If we make the not unwarrantable assumption that the intervals between the Blakeney dune ridges are approximately proportional to the intervals of time between their formation we obtain the following values:

Years	% Rate of leaching
5-80	0.25
80-160	0.67
160-235	1.06
235-340	0.63

It is at once apparent that the rate of leaching is at first very different in the two areas, being about 0.72 per cent. per annum at Southport during the period corresponding to 0.25 per cent. per annum at Blakeney, but despite this discrepancy in the early phases we find that in the later stages the rate of loss in proportion to the amount of carbonate present is very similar in the two areas, showing that the carbonate content and not the rainfall limits the rate of leaching. Making due allowance for the approximations on which these data are based it seems probable that the rate of leaching in the later stages is mainly determined by the amount of carbonate present even in different dune systems; a suggestion which, if true, implies either that the particles in old dunes generally assume such a shape that surface and volume diminish approximately in the same proportion, or more probably that the greater part of the carbonate is contained in vegetable remains.

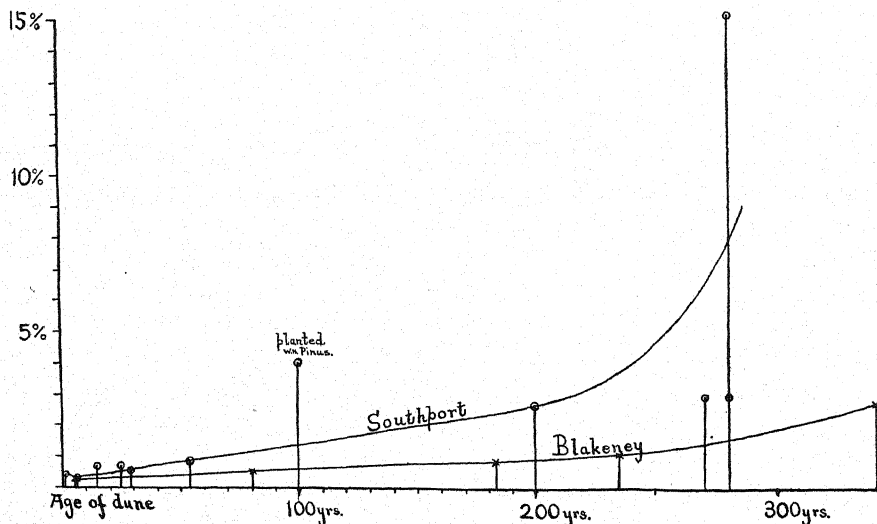


FIG. 2. Increase of Organic content of Dunes with increase of age.

The organic contents at Southport show increase with age, the only outstanding figure<sup>1</sup> being that for ridge (f), where the abnormally high value for the position in the series is doubtless due to the proximity of a pine plantation. Compared with Blakeney the values are high and the rate of

<sup>1</sup> The higher figure for ridge (a) than for ridge (b) is no doubt due to the fact that in embryo dunes the organic material is mainly derived from drift and not from the vegetation *in situ*.

increase is also more rapid (cf. Fig. 2), features possibly associated with the higher rainfall.

The chief difference in the dune soils of the two areas would appear to be the low calcium content at Blakeney and the much higher content in this respect at Southport, a difference which is reflected in the frequent presence of calcicoles in the latter area, often in some abundance, and their absence, so far as typical representatives are concerned, from Blakeney. As the writer has already pointed out<sup>1</sup>, many plants characteristic of chalk or limestone soils in this country probably prefer calcareous soils on account of the physical conditions, but their absence from Blakeney, where the rainfall is lower, indicates that chemical rather than physical differences are involved.

This is perhaps even more emphasised by the frequency of *Chlora perfoliata*, *Carlina vulgaris* and *Gentiana campestris*, in some of the wet "slacks" at Southport. Analyses of the soil from these shows that though the water-content and other physical properties are very different from those of the dunes bearing a calcicole vegetation, yet they agree in the presence of a high proportion of calcium carbonate, as is shown by the following data:

Dune Slack, Ainsdale (*Chlora perfoliata*, c.; *Inula conyza*, *Gentiana campestris*, *Carlina vulgaris*):  $\text{CaCO}_3$  1.46-13.9, pH 7.5-7.6.

Young Slack, Freshfield:  $\text{CaCO}_3$  1.40-2.6 pH 7.2.

Old Slack, Freshfield (*Chlora perfoliata*, *Gentiana campestris*, *Gentiana amarella*):  $\text{CaCO}_3$  3.05-3.7, pH 7.5.

The high calcium content in the old slacks, as compared with the low content of the old dune ridges between which they lie, is of course comparable to the contrast between the soil conditions on the summit of a wooded ridge and at its foot<sup>2</sup>.

As we have seen, Southport dunes have a much higher calcium content than those at Blakeney, but the figures for the former are much surpassed by those obtained from dune samples taken at Whitford Burrows in S. Wales. Here the yellow dunes yielded a carbonate content of from 11.8 to 13.5 per cent. and the older phases 3.2 per cent. With such high values it is not surprising that calcicolous species are frequent, amongst those present where the soil samples were taken being: *Carlina vulgaris*, *Gentiana amarella*, *Chlora perfoliata*, *Linum catharticum*, *Polygala oxyptera*, *Geranium sanguinum*, *Lithospermum officinale*, *Rubus caesius* and *Echium vulgare*; also the calcicole moss *Camptothecium lutescens*.

On the young dunes at Borth-y-Gest in N. Wales, where calcium carbonate contents of from 1.0 to 1.8 per cent. were obtained, there were present, *inter alia*, *Carlina vulgaris*, *Linum catharticum*, *Anthyllis vulneraria* and *Erigeron acre*. Some way inland sandy soil occurs with *Spiranthes autumnalis* and *Gentiana campestris*, so that it seemed probable that we here had an example

<sup>1</sup> "The significance of the calcicolous habit." This JOURNAL, 8, 1920.

<sup>2</sup> Cf. Salisbury, E. J. "Stratification and Hydrogen-ion Concentration of the Soil in Relation to Leaching." This JOURNAL, 9, 220-40, 1922.

of these normally calcicole species persisting on an old leached dune soil. Analysis showed, however, that the carbonate content was still as much as 0.3 per cent. Whether the maintenance of so high a content in a dune of presumably considerable age is a consequence of a high initial content or of rejuvenescence consequent upon differential wind action<sup>1</sup> we have no means of deciding, though the low values for the early phases examined support the latter alternative.

Samples of sand from dunes at Bundoran (Donegal) for which I am indebted to Mr Diver, show a much higher carbonate content than any examined from this country, probably due to the presence of large numbers of shells of *Helix nemoralis* whose comminuted fragments become incorporated with the sand. The average carbonate content of all the samples was 11.4 % with a minimum of 9.0 % and a maximum of 16.9 %. The high values, even in samples collected some distance from the shore, point to the possibly great importance of mollusca in retarding the process of leaching.

The data here presented show that the initial condition in dune soils exhibits a wide range of variation as to carbonate content, the high values being associated with a vegetation rich in calcicole species. But whether rich or poor in calcium initially the soil becomes very impoverished in this respect after a lapse of about 300 years and during these later stages the loss still continues at a fairly uniform rate of about 0.6 to 0.8 per cent. per annum, almost the whole of this calcium being probably present in the decaying organic matter.

All the dune areas of which soil samples have been examined support the view put forward by the writer that natural undisturbed soils in these latitudes tend to become more and more acid, to have an increasing organic content and a diminishing supply of available salts, of which calcium salts are the first to become markedly low in amount.

<sup>1</sup> Cf. Salisbury, E. J. "Soils of Blakeney Point," *l.c.* p. 396.

## NOTES ON PHOTOGRAPHING VEGETATION

By E. PICKWORTH FARROW.

THE phenomena associated with natural vegetation are usually extremely complex and it is very difficult to describe them at all adequately in words. Photographs, however, give a realistic pictorial representation of the vegetation and on this account they are invaluable when dealing with and describing the vegetation of any district.

The writer has had a good deal of experience in photographing vegetation for scientific purposes and by attention to some of the points mentioned in the following notes the percentage of successful results has been raised from about 30 per cent. to about 95 per cent. It is therefore thought that the ideas mentioned may be useful to other workers in this direction.

### NOTES ON APPARATUS.

#### A. *The Camera.*

*Type.* The most suitable kind of camera for this sort of work is probably the "Folding Pocket" type. The fact that the hinged baseboard completely covers and protects the lens and shutter and the bellows from injury and dirt when the camera is closed is a great advantage of this type of camera, and the type is extremely light and also compact when closed and, if made entirely of metal, it is very strong.

*Size.* The most suitable size of camera is probably the  $\frac{1}{4}$ -plate, as this size is sufficient to show detail well in contact prints and is just the right size for making contact lantern slides from portions of the negatives. The apparatus and material in this size are also relatively cheap and light to carry compared with the larger sizes and the plates are obtainable almost everywhere—anyhow, in the British Isles.  $3\frac{1}{2} \times 2\frac{1}{2}$  inches is too small to show detail well enough in contact prints and  $5 \times 4$  inches apparatus and materials are more costly and heavier to carry. Lightness will be found to be very important if the apparatus has to be carried about much for photographing the vegetation of extensive districts. For the above reasons  $\frac{1}{4}$ -plate is probably the most suitable size of camera for this kind of work.

*Extension.* It is essential that the camera should have double extension to the bellows and a convertible lens in order to be able to photograph near objects on a large scale, or full size, by using the complete lens, and large-scale views of distant vegetation by using the single components of the lens.

*Lens.* Any lens which will give good definition all over the plate at f. 8 can be used for vegetation photography as it is but seldom that a larger

aperture than the above is required. It is, however, advisable to use an anastigmat lens, especially if the results may subsequently be required for blockmaking or for lantern projection, as these processes bring out the imperfections in an uncorrected lens. If the camera is also to be used for the purposes of general photography it is a great advantage to have an anastigmat lens working at f. 6 for photographing moving objects in dull weather. There is not so much point in having a lens working at a larger aperture than f. 6 on an ordinary  $\frac{1}{4}$ -plate camera owing to the small depth of definition and the resulting difficulty in focussing. The most generally suitable and convenient focal length for the lens on a  $\frac{1}{4}$ -plate camera will be found to be about  $5\frac{1}{2}$  inches. The lenses in the single components should be cemented so as to have as few air-glass reflecting surfaces as possible inside the lens, since these result in loss of light and diminished rapidity for a given aperture and blurring of the finer detail in the resulting photograph—particularly in the shadows. The mounts of most modern lenses have been reduced to the minimum size for the sake of portability, and it will be found a great advantage to use an attachable lens hood since this cuts off a large amount of extraneous light and makes the resulting photographs far brighter than they would otherwise be.

*Shutter and Release.* Quite a simple shutter will do for photographing vegetation provided that it has a good "bulb" release. It is, however, a great advantage for the mechanism of the shutter to be completely enclosed in order entirely to prevent the possible ingress of dust and sand when travelling. If the camera is also to be used for general purposes it is a great advantage to have a high speed sector shutter such as the "Compound<sup>1</sup>," "Velosto" or "Koilos." In any case it is essential to have a flexible release attached to the shutter in order to reduce the vibration when making the exposure.

#### B. *Accessories.*

*Stand.* It is necessary to have a good strong stand for the camera. Wooden stands are preferable to the telescopic metal tripods, as they are usually much stronger and more rigid and sand is apt to get between the telescopic tubes of the latter and spoil their working. Also telescopic metal tubes are liable to be dented and become unworkable. It is a good plan to have a  $\frac{1}{2}$ -plate camera stand for a  $\frac{1}{4}$ -plate camera, as it is stronger and taller and gives a more natural viewpoint. The writer has found the "Jaynay" stand very satisfactory. The camera can be rotated independently of the stand and the sliding lower legs are useful for adjusting the height of the camera without moving the stand.

*Slides.* Single metal slides are probably the most simple and convenient devices for carrying the plates. When using these there is less risk of con-

<sup>1</sup> The latest model of the former "Compound" shutter is called the "Compur," the chief difference being that the latter has a mechanical regulating mechanism instead of the air brake regulating mechanism of the "Compound," thus avoiding the slight irregular variations to which air brake mechanisms are apt to be subject. The "Compur" may be stated to be the finest "between-lens" shutter obtainable.

fusion and double exposures than with book-form dark slides. If desired one can carry only a few of the slides at a time, thereby reducing the total weight of the apparatus, but it is necessary or at least advisable to have at least one dozen slides for most purposes.

Plates are more suitable than films for photographing vegetation as they are obtainable in a much greater variety of speeds and in various orthochromatic qualities. Possibly, however, if one were travelling in distant lands the greater lightness and portability of films might outweigh the above-mentioned advantages of plates.

*Case.* A good strong camera case with long shoulder straps is essential for carrying the camera and slides and for protecting them from injury in travelling.

*Orthochromatic Plates and Screen.* With ordinary plates the various shades of green of different kinds of vegetation all come out a fairly uniform dark colour in which it is difficult to differentiate the different colours of the various kinds of plants. This can be avoided by using orthochromatic plates and a yellow orthochromatic screen and, on this account, such plates and an ortho-screen should always be used in photographing vegetation in order to show up the various shades of green and enable one to differentiate the different kinds of plants. Another advantage of using a yellow ortho-screen is that it largely cuts out the blurring effects of bluish mist in the distance and renders the distant vegetation far clearer than it would otherwise appear.

It is better to purchase an ortho-screen which increases the exposure five times rather than an eight-times screen because a five-times screen used in conjunction with simple orthochromatic plates is sufficient for most purposes and does not increase the exposure so much, and it can be used in conjunction with self-screened varieties of ortho-plates for obtaining the effect of a ten-times screen if it is desired to secure still greater differentiation in the greens. It is a good idea to have a small pocket for the screen stitched inside the camera case so that the screen is always handy and with the camera and is never forgotten and left at home.

*Exposure Meter.* It is very advisable to get into the habit of always using an exposure meter for determining the exposure as the employment of these secures a much greater uniformity of success. Exposure calculators which depend on time of year, time of day, kind of sky, etc., are unreliable (especially when travelling abroad) and it is greatly preferable to use an exposure meter in which the required duration of the exposure is determined directly by the time of exposure required to darken a specially sensitised actinometer paper to a prearranged tint.

It is also preferable to use an exposure meter in which the two temporarily unalterable factors, viz. speed of plate and intensity of light are set opposite one another on the scales so that one can read off the corresponding values of the two voluntary variables—viz. size of diaphragm and duration of exposure

—directly and can decide which diaphragm and which exposure to use according to the circumstances without having to reset the scales of the exposure meter which is necessary on inferior types. The “Wynne” Hunter type meter and the “Imperial Exposure Meter for Bright Light” are both very good. In any case some kind of actinometer is essential or at least very advisable. It is the chief thing in photography and after using an actinometer one would never be without it.

#### NOTES ON PROCEDURE.

*Loading Slides.* It is advisable always to shake and dust the dark slides very carefully before loading them up with the plates. Especially if one is using very rapid orthochromatic plates be very careful to have a ruby light and not to expose the plates to it any more than necessary.

Photographs of vegetation may subsequently be required for making half-tone blocks and it is very desirable that they should be as far as possible perfect and free from scratches right up to the margins. On this account one's fingers should be very clean before handling the plates and as far as possible they should be handled only by the edges. This warning applies especially when loading single metal dark slides which are often more difficult to load than those of the book form.

*Cleaning Camera.* It is very advisable to dust and clean and adjust all the parts of the camera and to dust and clean the inside of the bellows and the inside of the camera case before starting out on each day's photography. It is very surprising how quickly dust, small plant fragments, fern fronds, sand, etc., can collect on and inside the camera and camera case. If one knows that all the parts of the camera and apparatus are perfectly clean and in good order before starting out for the day, one's mind is at rest about these matters and this is a great encouragement to turn out good work.

*Viewpoint.* When something is met which it is desired to photograph great attention should be paid to finding out the most suitable viewpoint from which to take the particular subject so as to show as much as possible, and give it in as good a perspective, and on as large a scale as possible. The camera lens should be placed as far as possible in a normal position and direction which a human eye would occupy in viewing the object being photographed as this tends to give the most natural effect. Objects look very different on the focussing screen however from what they do with the naked eye and on this account the final selection of the viewpoint should always be done, not by using the view finder, but by viewing the object on the focussing screen. This process is rendered much easier if the camera is mounted on a stand and on this account, as well as for other reasons, all photographs of vegetation, even if snapshots, should be taken if possible on a stand.

*Focussing.* After having selected the most suitable viewpoint focussing is the next thing to do. This is best done at the full aperture of the lens, focussing



on the principal portions of the subject and using a differential method, i.e. rack the camera out slightly until the image on the focussing screen just becomes blurred and then rack it in until the image becomes clear and then just equally blurred again and then take as the correct one the position approximately intermediate between these two extreme positions.

*Diaphragm and Exposure.* After having selected the most suitable viewpoint and focussed the next thing to do is to determine the most suitable diaphragm and exposure for the given make of plate and intensity of light by consulting the exposure meter.

In determining which diaphragm and exposure to employ a good rule to follow is to *use as small a diaphragm as possible*, although this necessitates increasing the exposure. The advantages of using a small diaphragm in photographing vegetation are immense—any ill effects of slight errors in focussing are enormously reduced and very great depth of definition is secured, showing up the near and distant vegetation equally sharply. The advantages of equal sharpness of near and distant vegetation is especially great if it is subsequently wished to make lantern slides. The writer generally employs f. 32, f. 45 and f. 56. The only thing which may prevent one from using a very small stop is that the vegetation may be moving owing to being blown about by wind, but the above advantages of using a small stop are so great that it is especially advisable to select as far as possible a calm day for this work.

*Preparation for Exposure.* After having determined the best stop and exposure, attach the ortho-screen to the lens, multiplying the exposure accordingly.

After this, the next thing to do is to *attend most carefully to the shutter*. This is especially necessary if one is using a rather complicated sector shutter such as the "Compound" or "Compur." It is very annoying to find that one has withdrawn the sheath of the dark slide before having closed the shutter after focussing or to make the exposure for a small stop having forgotten to close the diaphragm from full aperture. Therefore attend very carefully to the shutter and set the diaphragm to the prearranged value.

As fairly small apertures and an ortho-screen are being used short instantaneous exposures will seldom be employed and the shutter will usually be worked either at "time" or "bulb." It is much better to get into the habit of setting the shutter at "bulb" as this causes the shutter to close from the open "time" position used in focussing and obviates the risk of withdrawing the sheath of the dark slide with the shutter still open. Another advantage of always using the shutter set at "bulb" with a flexible release is that there is much less vibration than with the double impulse required for a "time" exposure. Shutters usually work much more gently in the "bulb" position. Also when the shutter is being used at "bulb" it is being controlled much more definitely and directly by the mind and hand and one knows much more definitely whether it is open or closed at any instant. This is a great advantage

when making a divided exposure in case a gust of wind interrupts the period of exposure required. After setting the shutter it is a good plan to sight along the edge of the baseboard of the camera and notice the spot where this projected line falls on the vegetation in front before placing the dark slide in the camera and withdrawing the sheath, so that, in case the camera has been slightly rotated by the latter processes, it can be gently set back to its original position without again examining the focussing screen.

The dark slide is placed in the camera and its sheath gently withdrawn. As photographs of vegetation are often taken in brilliant sunlight it is advisable to form a habit of always covering the rear portions of the camera with the focussing cloth in order to prevent the possible fogging of the plate by any internal leakages of light.

*Making the Exposure.* The apparatus is now ready for making the exposure and in case it is a gusty day it is a good plan not to be too impatient and make the exposure quickly but to *wait until the wind stops*. If one makes the exposure quickly during wind it often appears to happen that a period of great relative calm follows immediately after the exposure has been finished. By waiting some time, if necessary, before making the exposure the annoying element of chance in this respect is reduced and there is a greater likelihood of a short calm period intervening.

For measuring the exposure when using an actinometer it is greatly preferable to obtain scientific precision by using a stop watch, but if these do not happen to be available it is useful to know that the period required to count "one-two-three-four-five-six-seven-eight-nine" very rapidly represents approximately a second. One's rate of counting can previously be carefully standardised by comparison with a watch and the required number of seconds' exposure can be given by carefully repeating these numbers at the uniform standardised rate and ticking off the respective seconds by bending down one's fingers until the required exposure has been given.

An advantage of this method over exposing by means of a watch is that one can keep one's eyes on the vegetation which is being photographed all the time during the exposure without having to look at the watch, and in case a gust of wind commences to move the vegetation the exposure can immediately be stopped (especially with the shutter used at "bulb") and can be resumed and interrupted again for the necessary period after the conditions have calmed down.

If this method of counting seconds is used for measuring the exposure it should also be used for measuring the time required for the exposure meter paper to darken to the required tint, for any factorial error which might otherwise be introduced into the exposure thereby cancels out and an almost exact exposure is obtained.

Correct exposure is, as is well known, probably the chief point in successful photography. Especially when photographing vegetation in which detail is

required in the greens it is advisable to over-expose slightly rather than under-expose, for most plates have a fair amount of latitude; and although a slightly over-exposed negative takes a little longer to print it will eventually give the required detail, whereas an under-exposed negative will never give the required detail and is comparatively worthless. After having made the exposure immediately introduce the sheath into the dark slide, and at once withdraw the latter from the camera and place it carefully in the camera case.

*After the Exposure.* It is very advisable to treat dark slides containing plates (especially exposed plates) extremely gently and carefully, for after a plate has been carefully exposed it is difficult to estimate how valuable a negative may subsequently be produced from the contents of the dark slide.

It is very important to have some method of indicating whether the contents of a dark slide have been exposed or not. With some slides this can be indicated by putting the sheaths in the reverse way round. Other slides have tablets attached to them for noting whether the contents have been exposed or not. Slides can also be kept in different compartments or kept apart by a dividing arrangement to indicate whether they are exposed or not. In any case it is most important to have a reliable method of differentiating between the two classes. It is also strongly advisable always to keep the slides in their proper numerical order as this helps to avoid mistakes.

After an exposure has been made, it is usually better to remove the camera from the stand, place the ortho-screen in its pocket and fold the camera up and place it in its case rather than carry the camera exposed on its stand in the expectation that another photograph will quickly be required. If the camera be carried exposed on its stand in this expectation it will often happen that a long distance will be traversed before another photograph is required and in the meantime the exposed apparatus may get damaged.

It is a good plan to write the above processes out briefly on a card in the proper order and keep it in the camera case for a time and get into the habit of performing the various details in a fixed order like a machine by one's unconscious mind, so that uniformity of success and mechanical certainty in one's photography is secured and the conscious mind is eventually left entirely free to occupy itself with those important matters which cannot be dealt with automatically, such as the selection of the subject and the selection of the viewpoint.

The exposed plates can be developed in the evening after the day's work. It is advisable to develop plates as soon as convenient after exposure and it is a good plan to develop exposed plates fairly frequently, especially when travelling, so as to make sure that the photographic apparatus is working perfectly and that correct exposures are being given for the different kinds of subjects and so that the exposure factors for different kinds of subjects can be slightly varied if considered advisable. For this purpose it is a good plan to make previous careful notes of the light and exposure, etc., when each

photograph is taken. But notes on the ratio of these two factors are not so necessary when using the scales of an actinometer exposure meter, and it is sufficient to record the respective ratios of the exposures actually given to ones indicated by the meter. Small ruby lamp attachments are obtainable for fitting to the small electric pocket flashlamps which are in common use and these form extremely handy and useful dark room lamps for plate changing, etc., when travelling. If one is using panchromatic plates, green safelight paper is obtainable and can be fitted inside the flashlamp case over the bulb.

*Keep to one kind of Plate.* It is most advisable to stick to one make and speed of plate and one kind of developer as far as possible, as non-variation in these factors greatly helps to secure uniformity of success. Red does not usually enter largely into photographs of vegetation and panchromatic plates which are sensitive to red as well as to the greens and other colours are not worth the extra trouble and expense over good orthochromatic plates and there is the added difficulty in developing them. It is very advisable always to use backed plates as these give clearer horizons and are frequently necessary in woodland photography where high lights and strong contrasts often occur at the sky portions. It is very advisable to employ ortho-plates of very rapid quality as these enable one to use as small a diaphragm and as short an exposure as possible. The exposed plates must be fully developed so as to bring out all the detail in the greens, but they must not be over-developed or the contrast will be too great.

*Developing.* It is advisable to use the factorial method of development with solutions of known strength at a known temperature and the "time of development" factor can then subsequently be slightly varied as this is considered advisable. Probably pyro soda is on the whole the most satisfactory developer and it can be carried in powder form when travelling—or to save time in dissolving powders a concentrated single solution developer can be used diluted to a known strength.

*Printing.* The above notes are solely concerned with the production of a high percentage of first-class negatives. Good negatives are the most fundamental requirements in successful photography and from them good photographs can be obtained by many different printing processes, and good lantern slides can also be made from them, whereas from poor negatives no printing process whatever will give good results. For ordinary contact photographs, probably bromide papers are the most convenient printing media, but for the subsequent production of half-tone blocks good prints by the old-fashioned silver printing out process—now almost obsolete—are probably unequalled.

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